ISSN 0097-3157

PROCEEDINGS OF THE ACADEMY OF NATURAL SCIENCES OF PHILADELPHIA

VOLUME 139 FOR 1987
ISSUED 28 DECEMBER 1987

SUBSCRIPTIONS

Subscriptions to the PROCEEDINGS are $26.00 per year.

New subscribers are entitled to a 15% discount off the regular price of any one special publication or monograph of the Academy.

Back issues of the PROCEEDINGS may be ordered at $26.00 for subscribers and $30.00 for non-subscribers.

Nineteenth century back issues of the Academy's JOURNAL containing historically and artistically valuable plates are available on a limited basis. Also available are the Academy's SPECIAL PUBLICATIONS and MONOGRAPHS Series (see inside back cover of this issue).

For availibility of back issues, price quotes, and subscription information, write:

Scientific Publications
The Academy of Natural Sciences
19th and the Parkway
Philadelphia, PA 19103

PROCEEDINGS

OF

The Academy of Natural Sciences

OF

PHILADELPHIA

VOLUME 139, NUMBER 1

1987

This One
058K-TWO-00HX

PHILADELPHIA
THE ACADEMY OF NATURAL SCIENCES
Founded 1812
Issued December 28, 1987

© 1987 Academy of Natural Sciences of Philadelphia

DANIEL OTTE, Editor
ALFRED E. SCHUYLER, Associate Editor
DONALD AZUMA, Assistant to the Editor

PRINTED IN THE UNITED STATES OF AMERICA

THE SHERIDAN PRESS

CONTENTS

SMITH-VANZ, WILLIAM F. The saber-toothed blennies, tribe Nemophini (Pisces: Blennidae): an update 1

ROSENBERG, GARY AND RICHARD E. PETIT. Ryckholt's Mélanges Paléontologiques, 1851-1862, with a new name for *Tudicula* H. & A. Adams, non Ryckholt 53

ROHDE, FRED C. AND RUDOLF G. ARNDT. Two new species of pygmy sunfishes (Elassomatidae, *Elassoma*) from the Carolinas 65

ROBACK, SELWYN S. AND WILLIAM P. COFFMAN. Results of the Nepal alpine zone research project, Chironomidae (Diptera) 87

ROBACK, SELWYN S. The immature chironomids of the eastern United States IX. Pentaneurini - Genus *Labrundinia* with the description of some Neotropical material 159

ROBACK, SELWYN S. New species of *Labrundinia* from Colombia (Diptera: Chironomidae: Tanypodinae) 211

VOLKMER-RIBEIRO, CECILIA AND ANNA TRAVESET. Annotated catolog of the type specimens of Potts' species of freshwater sponges 223

ROBBINS, MARK B., ROBERT RIDGELY, THOMAS S. SCHULENBERG, AND FRANK B. GILL. The avifauna of the Cordillera de Cutucú, Ecuador, with comparisons to other Andean localities 243

MAHONEY, RONALD K. AND CHARLES W. REIMER. Current status of the type collection (Bacillariophyceae) in the Diatom Herbarium, The Academy of Natural Sciences of Philadelphia . . . 261

STONE, BENJAMIN C. AND ANTON WEBER. A new species of *Phyllagathis* (Melastomaceae) from the Endau-Rompin proposed national park, Malaysia 307

OTTE, DANIEL. African Crickets (Gryllidae). 9. New genera and species of Brachytrupinae and Gryllinae 315

OTTE, DANIEL, RICHARD D. ALEXANDER, AND WILLIAM CADE. The crickets of New Caledonia (Gryllidae) 375

BÖHLKE, E. AMD ALBERTO BRITO. *Gymnothorax bacalladoi*, a new moray from the Canary Islands (Pisces: Muraenidae) 459

HOAGLAND, K. ELAINE AND GEORGE M. DAVIS. The succineid snail fauna of Chittenago Falls, New York: taxonomic status with comparisons to other relevant taxa 465

Robertson, Robert. Virginia Orr Maes (1920-1986): biography and malacological bibliography 527

ADVICE TO AUTHORS

The *Proceedings* accepts papers in the areas of systematics, taxonomy, evolution, biogeography, and ecology. Although most manuscripts contain analyses of new data, succinct reviews and speculative or theoretical works that make major contributions are not discouraged. Authors must deposit type specimens, and/or voucher material to document their work, at The Academy of Natural Sciences or other recognized repositories prior to publication. All papers will be reviewed by at least two referees.

Manuscripts must be in English, written in a concise style, and double-spaced throughout. They should include title page, abstract, text, acknowledgments, literature cited, figure captions, footnotes, and tables in that order. The title page must include the title, name(s) of author(s), and complete address(es). The abstract not exceeding 200 words should summarize the pertinent points of the paper, including the major conclusions. It should be followed by up to 10 key words and a shortened title of less than 40 characters.

Primary headings should be centered on the page; secondary headings should be indented as for standard paragraphs and separated from the text with a period. In systematic headings, names of genera should be centered on the page and names of species should be flush left. Do not underline or italicize names of genera or species when they are in systematic headings. Synonymies may follow the short form: name, author, date, page, figure. Include full references in "Literature Cited."

Measurements must be in metric units. Numbers one through ten should be spelled out, unless used in combination with a larger number. Scientific names should appear in full with authors' names when first used. Spell out authors' names completely.

Figures should be separate from the text. Originals should be either on heavy mounting board, or in the form of glossy prints of professional quality. The author should proportion the illustrations so that they can be reduced to one- or two-column width (2⅝ inches or 5½ inches, respectively, for the *Proceedings;* column depth 7⅝ inches). Full-page illustrations should allow space for a legend. Use a lettering device to place letters, numbers, or labels on the illustrations; typed labelling is unacceptable. Refer to numbered figures consecutively in the text. *Figure Captions* and *Tables* should be typed on pages separately from the text. Large tables (>1 page) and complex formulae should be pasted up as a single sheet of copy. Avoid long captions and abbreviations.

In the "Literature Cited" section, spell out all journal and book names completely. Use the colon-parentheses system for volume, number, and page citations:

UZZEL, T., R. GÜNTHER, AND L. BERGER. 1977. *Rana ridibunda* and *Rana esculenta:* a leaky hybridogenetic system (Amphibia Salientia). Proceedings of the Academy of Natural Sciences of Philadelphia 128(9):147–171.

SOKAL, R. R. AND F. J. ROHLF. 1969. Biometry, the principles and practice of statistics in biological research. W. H. Freeman and Company, San Francisco. xxi + 776 pp.

In citing references within the text, do not place a comma between names of authors and date, e.g., Jones 1981 instead of Jones, 1981. For other details of format, consult a recent issue of the Proceedings or Notulae Naturae. Provide the editor with the original plus two copies of the manuscript, including illustrations.

Authors will receive page proof, and may also be queried by the editors during the initial stages of editing. Author's alterations made after page proof is received will be billed to the author.

Send manuscript and correspondence to:
Editor, Scientific Publications
Academy of Natural Sciences of Philadelphia
19th and the Parkway
Philadelphia, PA 19103

PUBLICATION ANNOUNCEMENT

The Academy of Natural Sciences announces the publication of Special Publication Number 15 in July 1985:

Morphometrics in Evolutionary Biology: the Geometry of Size and Shape Change with Examples from Fishes

F. L. BOOKSTEIN, B. CHERNOFF, R. L. ELDER, J. M. HUMPHRIES, G. R. SMITH, AND R. E. STRAUSS

Written for researchers, teachers, and students in those branches of biological and medical sciences concerned with shape-change in organisms. This book explores mathematical and statistical approaches to the relationships between allometry, form-change, ontogeny, phylogeny, homology, evolution, morphological complexity and taxonomic divergence. It presents new methods for quantifying shape-change, reconstructing evolutionary and ontogenetic changes in form, and for multivariate statistical analysis of population variation. Helpful tools are introduced for use of computers in selecting, acquiring, transforming and analyzing data from biological shapes. The foundations and methods of morphometrics are discussed in relation to statistical and biological principles.

	$22.00 cloth
	$14.00 paper
Plus postage:	$ 1.00 U.S. and Canada
	$ 2.00 other

Order from: Scientific Publications, Academy of Natural Sciences of Philadelphia,
19th and the Parkway, Philadelphia, PA 19103

Proceedings of The Academy of Natural Sciences of Philadelphia 139: 1–52, 1987.

The Saber-Toothed Blennies, Tribe Nemophini (Pisces: Blenniidae): an Update

WILLIAM F. SMITH-VANIZ
Department of Ichthyology
The Academy of Natural Sciences of Philadelphia
19th and the Parkway, Philadelphia, PA 19103

ABSTRACT.—New information (distribution records, behavioral observations, taxonomy) is given for selected species of *Petroscirtes*, *Aspidontus*, *Xiphasia*, *Meiacanthus*, and *Plagiotremus*. Revised keys are given to the species of *Meiacanthus* and *Plagiotremus*. Seven new species of *Meiacanthus* are described and illustrated: *M. abditus* (Sulu Archipelago), *M. crinitus* (Irian Jaya), *M. naevius* western Australia), *M. limbatus* (Bismarck Archipelago), *M. vicinus* (Sulawesi), *M. luteus* (Australia), and *M. tongaensis* (Tonga Islands). *Meiacanthus ovalauensis* (Günther), previously recognized as a subspecies of *M. atrodorsalis* (Günther), is accorded full specific rank. *Lembeichthys celebesensis* Herre is synonymized with *Plagiotremus spilistius* Gill. All known mimetic associations involving species of *Meiacanthus* are briefly summarized, including some new observations. [*Aspidontus*, biogeography, Blenniidae, fishes, Indo-Pacific, *Meiacanthus*, mimicry, new species, *Petroscirtes*, systematics, *Xiphasia*]

In the decade since publication of my monograph of the blenniid tribe Nemophini (Smith-Vaniz 1976), many important observations and collections of Indo-Pacific reef fishes, including saber-toothed blennies, have been made. Study of this new material has resulted in recognition of new species that were previously misidentified, synonymization of one nominal species, and, as predicted, the discovery of several new species that until recently had not existed in any museum collection. As detailed in the present paper, 48 species of Nemophinine blenniids are now recognized, with changes in number of species occurring in two genera as follows: increase in *Meiacanthus* from 16 to 24 and decrease in *Plagiotremus* from 11 to 10. New distributional records, supplemental descriptive data, and behavioral observations are also given for some previously described species.

To facilitate comparisons, sequence of presentation of taxa corresponds to that given in my monograph. Methods for counts and measurements are also as described there. Material lists include capture locality (usually abbreviated), followed by institutional abbreviation, catalog number, and the number of specimens and size range, in parentheses, as mm standard length. Institutional abbreviations are the same as those used in 1976 and agree with those recommended by Leviton et al. (1985).

Genus Petroscirtes Rüppell

Petroscirtes xestus Jordan and Seale

Although *P. xestus* is widely distributed throughout much of the Indo-Pacific, the only previous Australian record of the species was from the Great Barrier Reef. The specimen cited below is the first record of *P. xestus* from Western Australia.

NEW MATERIAL. WESTERN AUSTRALIA: Rowley Shoals, Clerke Reef, WAM P.27670-003 (1, 39.0).

Petroscirtes springeri Smith-Vaniz

Originally based on a single 49.7 mm SL specimen from Taiwan, Yatsu et al. (1983) redescribed *P. springeri* on the basis of four additional specimens (51.7–76.5 mm) from southern Japan. The new specimens generally agree with the original description except as follows (characters for the holotype given first and followed, in parentheses, by those of the Japanese specimens): segmented dorsal- and anal-fin rays each 21 (21–22); upper incisors 24 (25–27), lower incisors 30 (30–33); one pair of interorbital, predorsal, and nuchal cirri (none); symphyseal mandibular cirri multifid (simple to multifid); middle symphyseal mandibular cirri multifid (simple to bifurcate); rear mandibular cirri bifurcate (simple); length of 2nd dorsal-fin spine 9.5% SL (8.9–13.3); length of pelvic fin 12.1% SL (11.2–15.8); length of caudal fin 25.9% SL (19.3–30.7). I consider these differences to be within the expected range of individual variation.

Petroscirtes breviceps (Valenciennes)

Arai and Ida (1975) illustrated *Meiacanthus kamoharai* and a single specimen of *P. breviceps* (which they identified as *Dasson* sp.), both from Tanegashima Island, Japan, and commented on their closely matching color patterns. In referring to the previous reference, Yatsu et al. (1983) noted that *P. breviceps* has been reported (Springer and Smith-Vaniz 1972) as a possible mimic of *M. grammistes* and that establishment of a second mimetic relationship with the closely related and allopatric *M. kamoharai* might be expected.

Petroscirtes marginatus Smith-Vaniz

The second known specimen, a recently collected male, of *P. marginatus* is here compared with the 39.2 mm SL female holotype. The Indonesian locality and deep-water trawl capture of this rare blenniid are both significant. The holotype, probably collected during the voyage of the H. M. S. "Samarang" (Adams 1850), was reported to have come from "China." Most collections of *Petroscirtes* species are from depths shallower than 5 meters, with 18 m the maximum previously recorded. The Indonesian specimen agrees well with the original description, especially in details of its color pattern, in having a pair of mid-dorsal supratemporal pores, and in lacking posttemporal and orbital cirri. Only the following differences were noted (characters for the holotype given first and followed, in parentheses, by those of the new specimen): dorsal rays XI, 19 (X, 19); segmented anal rays 17 (18); vertebrae 13 + 22 (12 + 22); upper incisors 34 (43); lower incisors 34 (40); mandibular cirri absent (symphyseal and adjacent mandibular pore position each with a simple cirrus, both sides); length of 2nd dorsal-fin spine 9.8% SL (11.6); pelvic fin length 6.4% SL (6.9); outer lobes of caudal fin not elongate, 16.2% SL (elongate, 37.3). The difference in caudal fin length is undoubtedly due to sexual dimorphism, while the other differences are within the expected range of individual variation.

NEW MATERIAL. INDONESIA: Sumbawa, Saleh Bay (Teluk Saleh), ca. 08°30'S, 118°00'E, trawled in 180–300 m, sta. TGT 1891, 16 Jul 1981, NTM S.11920-020 (male, 49.1).

Petroscirtes variabilis (Cantor)

Although widely distributed in the western Pacific Ocean, until recently there were no reliable records of *Petroscirtes variabilis* from the Ryukyu Islands or Australia, except from the Great Barrier Reef. Yatsu et al. (1983) documented the occurrence of the species from the Ryukyu Islands on the basis of a single specimen from Ishigaki Island. The specimen cited below is the first Australian record of *P. variabilis* west of Cape York.

Based on examination of 14 adults obtained from Bolinao fish market, Luzon, Philippines, Ferraris and Murdy (1983) suggested that *P. variabilis* exhibits sexual dichromatism: females are sea-green dorsally and lighter below, and males are generally orange-brown. Gut contents of these specimens indicated that the species feeds on or near to the turtlegrass substrate, its usual habitat, with crustaceans forming the bulk of its diet. Four individuals had each ingested a single fish scale. Ferraris and Murdy (1983) also reported that in an aquarium *P. variabilis* spends most of its time hovering motionless in mid-water, in a vertical head-up orientation like that observed (Emery in Smith-Vaniz 1976) in the closely related *P. thepassi.* They hypothesized that lepidophagy might be an occasional feeding tactic of *Petroscirtes variabilis*. Its life coloration and vertical orientation among *Thalassia* blades would allow *P. variabilis* a close, undetected approach to potential fish prey.

NEW MATERIAL. AUSTRALIA: Coburg Peninsula, Danger Point Beach, NTM S.10445-001 (1, 29.2).

Petroscirtes ancylodon Rüppell

A previously unreported nuptial male, 104 mm SL, of *P. ancylodon* from Doha Bay, Qatar (USNM 217353), is the largest individual of the species known; the largest known female is 78.6 mm SL. As previously documented (Smith-Vaniz 1976), *Petroscirtes* males typically attain a larger size than females, perhaps owing to the selective advantage of large size in courtship display and intermale dominance relations in a promiscuous mating system.

Genus **Aspidontus** Cuvier

Aspidontus taeniatus Quoy and Gaimard, Figs. 1a-d

One of the best known examples of mimicry (aggressive mimicry involving three or more species, Wickler 1968) in fishes is that of the mimic blenny, *Aspidontus taeniatus*, and the cleaner wrasse, *Labroides dimidiatus* Quoy and Gaimard. This mimetic interaction, which does not include the pelagic prejuvenile ("*filamentosus*" form) of *taeniatus*, was described in detail by Randall and Randall (1960). The pronounced ability of *Aspidontus taeniatus* to alter its color pattern to closely duplicate those of geographically variable or alternative mimetic models is, however, only now beginning to be recognized.

Springer and Smith-Vaniz (1972) observed that individuals of *A. taeniatus* from the Red Sea and western Indian Ocean (*tractus* form, Fig. 1a) differ from other populations of the species in having a black bar on the fleshy pectoral-fin base. They also reported the existence of uniquely pale specimens of *A. taeniatus* (Fig. 1c) that are probable mimics of a similarly pigmented, apparently undescribed, species of *Coris* known only from the Marquesas Islands. Typically pigmented *A. taeniatus* also occur there but have not been observed to associate with the pale *Coris*. More recently, Russell et al. (1976) documented a mimetic association between a species of *Labroides* from Samoa and nearly identically pigmented individuals of *A. taeniatus* (Fig. 1d), both characterized by a large orange area on the posterior part of the flanks and an incomplete dark lateral stripe. Typical individuals of *A. taeniatus* were also observed mimicking *L. dimidiatus* at Samoa. Apparently the same species of *Labroides* (but with a yellow instead of orange flank), which may only be a color variant of *L. dimidiatus*, was recently collected, together with typical *L. dimidiatus*, at Rotuma (V. G. Springer pers. comm.). Only typical *A. taeniatus* were seen and collected at Rotuma but observations and collections were limited.

Genus **Xiphasia** Swainson

Xiphasia setifer Swainson

The single specimen of *X. setifer* cited

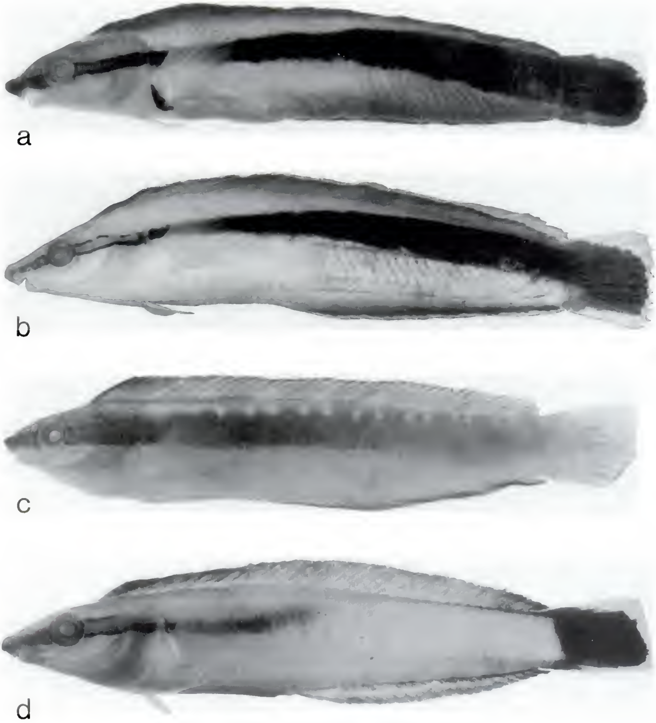


FIG. 1. *Aspidontus taeniatus*. **a**, USNM 204552, Red Sea, Sinai Peninsula, female, 61.5 mm SL; **b**, USNM 223425, Ponape, female, 70.3 mm; **c**, BPBM 10881, Marquesas Is., male, 66.1 mm; **d**, BMNH 1983.3.25.1067, Samoa, Tutuila Is., 49.5 mm, after Russell et al. (1976: pl. VII).

below is the first record of a member of the tribe Nemophini from the eastern Atlantic Ocean. The possibility that this record is erroneous seems unlikely as other typically west African fishes were taken at the same station, including the gobiid *Sufflogobius bibarbatus* (von Bonde) and soleid *Austroglossus microlepis* (Bleeker), both eastern Atlantic endemics. It is not too surprising that this eel-like, semipelagic blenniid has been collected outside the Indo-Pacific. As discussed by Penrith (1976), it is not difficult for inshore pelagic species to negotiate the Cape Barrier, either actively in the warm water outside the upwelled component of the Benguela Current system or passively in west- and northward-moving isolated eddies of Agulhas water.

NEW MATERIAL. SOUTH AFRICA: 29°06′S, 16°37′E; trawled in 108 m; 25 Jan 1986; R/N AFRICANA, cr. 28, sta. A2352; RUSI 25505 (1, 266).

Xiphasia matsubarai Okada and Suzuki

Previously the easternmost record of this blenniid was a single specimen from Alexa Bank, 11°40′S, 175°10′E, near Rotuma and somewhat north of the Pacific Plate margin. The two collections from American Samoa listed below extend the geographic range of *X. matsubarai* approximately 1200 km eastward.

NEW MATERIAL. AMERICAN SAMOA: Tutuila Is., off Fagasa, caught at surface under night light, ANSP 147875 (4, 206–241); Olosega Is., near Sili, handline in 26 m depth, BPBM 25304 (1, 236.8).

Genus **Meiacanthus** Norman

In order to facilitate comparison of the seven new species described herein, and to more conveniently report additional meristic data for relatively uncommon species, all species of *Meiacanthus* are included in Tables 1–4. Four of the 21 species of *Meiacanthus* found in the western Pacific region (including the western margin of the Pacific Plate) are known from single collections, and others appear to have relatively restricted distributions; thus, it is likely that additional new species await discovery. See discussion under *M. lineatus* species account. The number of *Meiacanthus* species known to occur in various Indo-Pacific localities is shown in Fig. 2. The following revised key to the subgenera and species of *Meiacanthus*, except the *M. atrodorsalis* complex (see Table 6), is given as an identification aid:

1a. Dark mid-lateral stripe forks at front of pectoral fin, with dorsal arm of fork extending through eye and ventral arm extending to gape; mandibular pores 2; lateral line absent; dentary gland positioned ventrally and encapsulated in dentary (western and central Pacific) .... *M. (Allomeiacanthus) ditrema* Smith-Vaniz

1b. Dark mid-lateral stripe, if present, not forked at front of pectoral fin; mandibular pores 3; short lateral line present; dentary gland positioned dorsolaterally and not encapsulated in dentary 2

2a. Dorsal-fin spines 6–10 (rarely 6); segmented dorsal-fin rays 20–24; mid-point of supratemporal canal typically ending in a pair of pores; dentary gland supported by dentary and articular and held in place laterally by flange of articular (western and central Pacific) .... *M. (Holomeiacanthus) anema* (Bleeker)

2b. Dorsal-fin spines 3–6 (rarely 6); segmented dorsal-fin rays 23–28; mid-point of supratemporal canal usually ending in a single pore; dentary gland supported solely by dentary and held in place laterally by flange of dentary (*Meiacanthus*) 3

3a. Adults with one or more conspicuous lateral stripes on body and/or belly and underside of head dark and strongly vermiculated 4

3b. Adults without lateral stripes on body (except Red Sea-Gulf of Aden endemic *M. nigrolineatus*, which has an oblique lateral stripe, see couplet 17a), and belly and underside of head not dark and strongly vermiculated 14

4a. Caudal fin heavily pigmented on dorsal and ventral margins and/or middle fin rays distinctly spotted; dark stripes on body interrupted posteriorly or replaced by conspicuous dark spots 5

4b. Caudal fin pale or with dark stripes restricted to proximal fourth of fin; dark stripes on sides clearly defined posteriorly (except in *M. naevius*, see couplet 8a) 6

5a. Ventral surface of head and belly uniformly pale (throat with 2 or 3 spots in some specimens); dark stripes on head approximately equal in width to pale interspaces (western and central Pacific) . . *M. grammistes* (Valenciennes)

5b. Ventral surface of head and belly dark or vermiculated; dark stripes on head, if present, approximately twice the width of pale interspaces (Japan and Ryukyu Islands) .... *M. kamoharai* Tomiyama

6a. Adults with two dark, lateral stripes in addition to one at dorsal body contour 7

6b. Adults with a single dark, lateral stripe in ad-

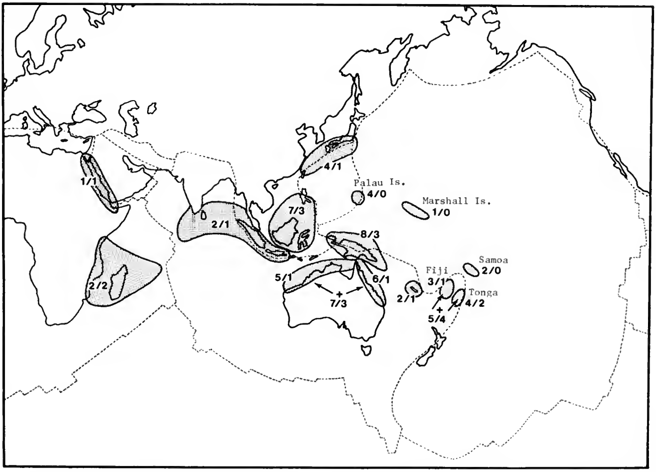


FIG. 2. Number of *Meiacanthus* species known to occur at various Indo-Pacific localities. The first number represents the total number of species known from an area; the number of endemic species is indicated by the second number; the numbers below a plus sign indicate values for two combined areas. Dashed lines denote margins of major lithospheric plates, based on Springer (1982).

dition to one which may occur at dorsal body contour 11

7a. Chin, including lower lip, broadly dark (Fig. 3c); anal-fin base with narrow, dark stripe (Bismarck Archipelago) . . . . . *M. limbatus* n. sp.

7b. Chin, including lower lip, pale or narrowly dusky; anal-fin base without narrow, dark stripe 8

8a. Caudal peduncle pale except for elongate basicaudal spot; distal half of dorsal fin pale posteriorly; pectoral-fin rays 12 or 13 (western Australia, Rowley Shoals) . . . . *M. naevius* n. sp.

8b. Caudal peduncle typically with two dark stripes that extend at least to caudal-fin base; distal half of dorsal fin with dark stripe; pectoral-fin rays 14–16 (except 12 or 13 in *M. crinitus*) 9

9a. Dark stripe on snout that extends through eye separated from margin of upper lip by pale area approximately equal to width of stripe, Fig. 3a (eastern Australia) . . . . *M. lineatus* (DeVis)

9b. Dark stripe on snout that extends through eye touches margin of upper lip 10

10a. Pectoral-fin rays 14 or 15; pale area above and adjacent to dark mid-lateral head stripe continues uninterrupted across snout (Fig. 3b); adult *males* with inner caudal-fin rays not elongated and interradial membranes not deeply incised (Sulu Archipelago) . . . . *M. abditus* n. sp.

10b. Pectoral-fin rays 12 or 13; pale area above and adjacent to dark mid-lateral head stripe, if continued onto snout, interrupted at mid-line; adult *males* with inner caudal-fin rays elongated (Fig. 10) and interradial membranes deeply incised (Irian Jaya) . . . *M. crinitus* n. sp.

11a. Dark lateral stripe not centered as it extends onto caudal fin, at most only dorsal margin of stripe aligned with center of fin (northern

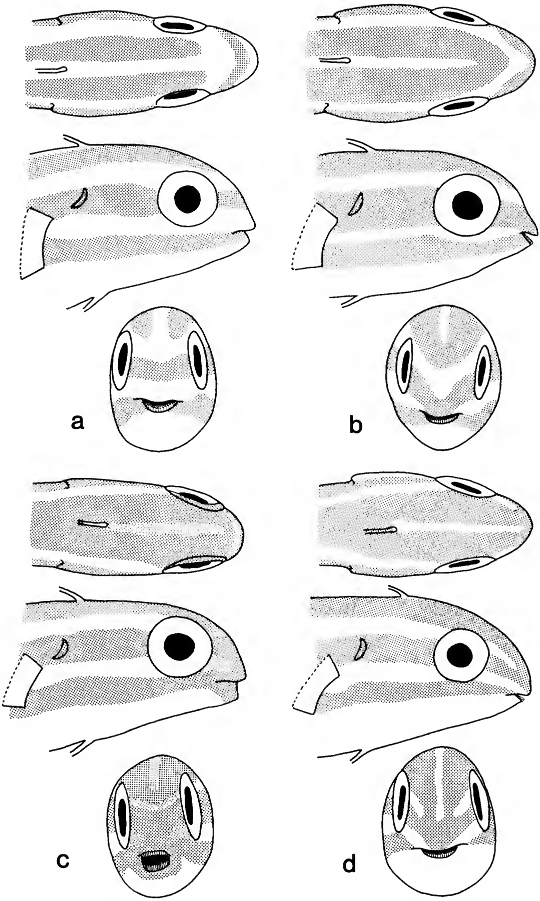


FIG. 3. Head color patterns in certain species of *Meiacanthus*. **a**, *M. lineatus*, USNM 211308, Australia, Heron Is., 38.5 mm SL; **b**, *M. abditus*, holotype; **c**, *M. limbatus*, holotype; **d**, *M. crinitus*, holotype.

Borneo and Palawan) .... *M. geminatus* Smith-Vaniz

11b. Dark lateral stripe approximately centered as it extends onto caudal fin 12

12a. Dorsal fin conspicuously bicolored, distal half of fin immaculate and basal half abruptly dark brown; width of dark stripe on snout distinctly narrower than width of stripe immediately posterior to eye (Fig. 4b); dark lateral stripe does not extend onto dorsal part of pectoral-fin base (Sulawesi) .... *M. vicinus* n. sp.

12b. Dorsal fin not conspicuously bicolored; width of dark stripe on snout not distinctly narrower than width of stripe immediately posterior to eye (Figs. 4c–d); dark lateral stripe extends at least slightly onto dorsal part of pectoral-fin base 13

13a. Pectoral-fin rays usually 13; dark lateral stripe extends conspicuously onto dorsal part of pectoral-fin base; in life, body coloration above dark mid-lateral stripe pale gray; adult *males* with inner caudal-fin fin rays elongated and interradial membranes deeply incised, Fig. 18b (Papua New Guinea and New Britain) .... *M. vittatus* Smith-Vaniz

13b. Pectoral-fin rays usually 15 or 16; dark lateral stripe extends very slightly onto dorsal part of pectoral-fin base; in life, body coloration above dark mid-lateral stripe bright yellow; adult *males* with inner caudal-fin rays not elongated and interradial membranes not deeply incised (Australia)...... *M. luteus* n. sp.

14a. Dark spot, approximately equal to pupil diameter, on ventral half of pectoral-fin axil (western and central Pacific) .... *M. atrodorsalis* complex (see Table 6)

14b. No dark spot on pectoral-fin axil........... 15

15a. Anal fin pale.............................16

15b. Anal fin dark............................ 19

16a. Outer lobes of caudal fin not elongated, middle rays longest; dark stripe extends from eye to origin of dorsal fin (Maldive Islands, Sri

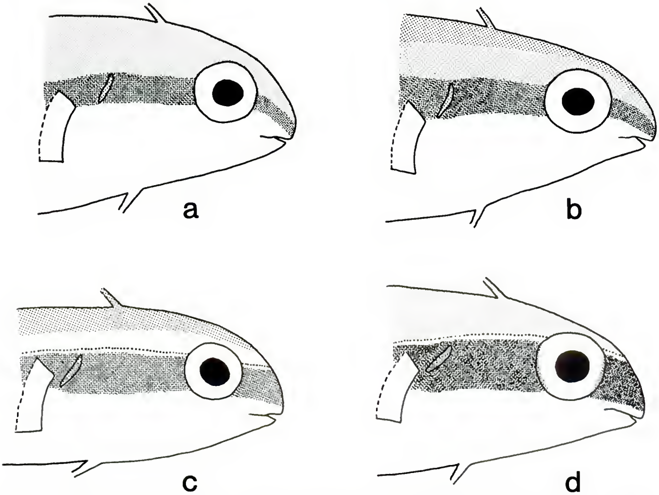


FIG. 4. Comparison of head stripes in the *Meiacanthus geminatus* species group. a, *M. geminatus*, USNM 218703, Philippines, Cuyo Is., 46.9 mm SL; **b**, *M. vicinus*, holotype; c, *M. luteus*, NTM S.11358-002, Darwin, 41.5 mm; **d**, *M. vittatus*, AMS I.20428-001, Port Moresby, 38.7 mm.

Lanka, and western Java Sea) . . . . *M. smithi* Klausewitz

16b. Outer lobes of caudal fin elongated, at least in adults; color pattern not as above. 17

17a. Narrow dark stripe extends obliquely from eye to upper margin of caudal peduncle or below posterior third of dorsal fin (Red Sea, including Gulfs of Aqaba and Aden) . . . . *M. nigrolineatus* Smith-Vaniz

17b. Color pattern not as above. 18

18a. Dorsal fin heavily and uniformly pigmented, except for pale tips of rays; posterior third of body uniformly pale (Cargados Carajos, western Indian Ocean) . . . . *M. fraseri* Smith-Vaniz

18b. Dorsal fin dark with central pale stripe; posterior third of body dark dorsally, and spotted or speckled in large specimens (Tonga Islands) . . . . *M. procne* Smith-Vaniz

19a. Caudal fin immaculate (African coast, Comoro Is. and Madagascar) . . . *M. mossambicus* Smith

19b. Outer lobes of caudal fin heavily pigmented 20

20a. Head and body with many dark speckles; pectoral-fin rays 14 (Solomon Sea and Osprey Reef, Coral Sea) . . . *M. reticulatus* Smith-Vaniz

20b. Head and body without dark speckles; pectoral-fin rays 15 or 16 21

21a. Outer lobes of caudal fin not distinctly darker than posterior fifth of body; head and body very dark except for pale wedge-shaped area (yellow-orange in life), base of which covers postorbital region of head (Fiji and Tonga Islands). . . . . *M. bundoon* Smith-Vaniz

21b. Outer lobes of caudal fin distinctly darker than posterior fifth of body; head and body uniformly light brown, at least in preservation (New Caledonia). . . . . . . *M. phaeus* Smith-Vaniz

Meiacanthus ditrema Smith-Vaniz

Meiacanthus ditrema is relatively common and broadly distributed, Fig. 5. As originally noted, this species tends to form schools and hover in the water column feeding on zooplankton. The following material all represents new locality records, including some eastern and western range extensions.

NEW MATERIAL. PHILIPPINES: Siguijor Island, 9°8′28″N, 123°29′40″E, ANSP 152367 (2, 25.4–33.3); Oriental Negros, off Bonbonon Point, 9°3′N, 123°7′E, USNM 220937 (1, 30.5), USNM 222109 (9, 17.5–36.1), ANSP 152368 (9, 13.6–26.2). WESTERN AUSTRALIA: Rowley Shoals, WAM P.27666-001 (15, 17.3–32.5), WAM P.28021-047 (1, 30.3). EASTERN AUSTRALIA: Escape Reef, 15°49′S, 145°50′E, AMS I.22586-013 (6, 13–30), AMS I.22633-023 (45, 9–31). TONGA ISLANDS: Tongatapu, BPBM 30876 (2, 37.1–40.6), BPBM 30879 (2, 33.9–37.7). AMERICAN SAMOA: Tutuila Island, Pago Pago Bay, USNM 222110 (2, 14.0–15.9).

Meiacanthus lineatus (De Vis), Figs. 7a, 8a

A Great Barrier Reef endemic, *Meiacanthus lineatus* occurs from Murray Island (9°55′S, 144°5′E) in Torres Strait southward to One Tree Island (23°30′S, 153°8′E) in the Capricorn Group. Smith-Vaniz (1976) erroneously considered *M. lineatus* to consist of two widely disjunct populations, but noted that the one available adult male from the Sulu Archipelago differed in certain respects from Australian males. Recent collections of several new, allopatric species with color patterns superficially similar to *M. lineatus* prompted reassessment of my identification of the Sulu specimens, and I now find them to represent a new species, *M. abditus* described below.

SPECIES COMPARISONS. The following species are here referred to collectively as the *Meiacanthus lineatus* species group: *M. lineatus*, *M. abditus*, *M. limbatus*, *M. naevius*, and *M. crinitus*. After this paper was completed I received a color photograph of what appears to be another undescribed member of the *M. lineatus* species group. The photograph, taken underwater at Flores Island (8°35′S, 122°13′E) by Rudie H. Kuiter, shows three fish in good focus but with different orientation. At least one individual has elongate inner caudal-fin rays (as in *M. crinitus*) and all have a head stripe pattern that is most similar to *M. abditus* but they differ from that species in other aspects of their color pattern, including lateral body stripes that terminate at the caudal-fin base (versus distinctly extending onto the caudal fin). The Flores *Meiacanthus* were seen only at

TABLE 1. Frequency distributions of dorsal-fin rays in species of *Meiacanthus*.[1]

	Dorsal-fin spines									Segmented dorsal-fin rays										Total dorsal-fin elements						
Species	3	4	5	6	7	8	9	10	$\bar{x}$	20	21	22	23	24	25	26	27	28	$\bar{x}$	28	29	30	31	32	33	$\bar{x}$
anema				1	10	223	17	1	8.0	13	146	88	4	1					21.3	9	147	88	8			29.4
ditrema		3	59	5					5.0			2	9	39	16	1			24.1	10	41	15	1			29.1
grammistes	9	155	3						4.0						51	103	12	1	25.8		55	100	12			29.7
kamoharai		10							4.0						1	5	4		26.3		1	5	4			30.3
lineatus		74							4.0						2	49	20	3	26.3		2	49	20	3		30.3
abditus		14							4.0							8*	6		26.4			8*	6			30.4
limbatus		1							4.0							1			26.0			1				30.0
crinitus	1	10							3.9						10*	1			25.1	1	9*	1				29.0
naevius		1							4.0							1			26.0			1				30.0
geminatus		21							4.0						1	15	5		26.2		1	15	5			30.2
vicinus		1							4.0							1			26.0			1				30.0
luteus	3	28							3.9							8*	20	3	26.9			10*	19	2		30.7
vittatus	1	23							4.0						5	11	8		26.1		5	12	7			30.1
nigrolineatus		100	7						4.1				2	32	65	8			24.7	31	67	9				28.8
mossambicus		3	22						4.9					1	14	9	1		25.4		2	14	9			30.3
fraseri		3	24						4.9					9	18				24.7		12	15				29.6
smithi	1	33	1						4.0					1	12	22			25.6	1	12	22				30.4
atrodorsalis	3	227	7						4.0						39	122	69	7	26.2		33	118	71	15		30.3
ovalauensis		53	1						4.0						1	5	38	10	27.1			6	38	10		31.1
tongaensis		18							4.0								7	11*	27.6				7	11*		31.6
procne		2	21						4.9						9	13	1		25.7			10	13			30.6
reticulatus			4						5.0							3	1		26.3				3	1		31.2
bundoon		1	13						4.9							5	8	1	26.7				6	7	1	31.5
phaeus		1							4.0								1		27.0				1			31.0

[1] When counts vary, those for holotypes of new species are indicated by an asterisk.

TABLE 2. Frequency distributions of vertebrae in species of *Meiacanthus*.[1]

Species	Precaudal vertebrae					Caudal vertebrae								Total vertebrae							
	11	12	13	14	$\bar{x}$	19	20	21	22	23	24	25	$\bar{x}$	32	33	34	35	36	37	38	$\bar{x}$
anema	141	108	1		11.4		5	56	115	68	6		22.1	8	121	108	13				33.5
ditrema	29	37			11.6			12	34	18	2		22.2		22	40	4				33.7
grammistes			23	142	13.9	1	67	81	15	1			20.7		2	82	71	10			34.5
kamoharai			9	9	14.0			4	5				21.9				4	5			35.6
lineatus		1	46	26	13.3		2	21	42	8			21.8			7	50	16			35.1
abditus		1	13*		12.9			1*	9	4			22.1			1*	10	3			35.1
limbatus			1		13.0				1				22.0				1				35.0
crinitus		2	8*	1	12.9	3	6*	2					19.9	4	5*	2					32.8
naevius				1	14.0		1						20.0			1					34.0
geminatus			18	3	13.1		1	9	11				21.5			8	18				34.6
vicinus			1		13.0			1					21.0			1					34.0
luteus		6	24*	1	12.8				10*	19	2		22.7				15*	14	2		35.6
vittatus			21	1	13.0		6	8	8				21.1		5	9	8				34.1
nigrolineatus		42	60		12.6		22	57	23				21.0	1	41	59	1				33.6
mossambicus			16	9	13.4			5	15	5			22.0			2	13	10			35.3
fraseri		9	18		12.7			4	20	3			22.0			10	17				34.6
smithi		11	23	1	12.7			26	9				21.3		7	22	6				34.0
atrodorsalis		73	156	7	12.7		8	56	120	46	5	1	21.9		14	81	113	25	3		34.7
ovalauensis		2	42	8	13.1			5	28	19			22.3			3	28	19	2		35.4
tongaensis		2*	16		12.9				2	16*			22.9				4*	14			35.7
procne			10	13	13.6			7	9	7			22.0				10	13			35.6
reticulatus			4		13.0				1	3			22.8				1	3			35.7
bundoon		2	12		12.9					3	9	2	23.9					5	7	2	36.8
phaeus				1	14.0				1				22.0					1			36.0

---

[1] When counts vary, those for holotypes of new species are indicated by an asterisk.

TABLE 3. Frequency distributions of anal- and pectoral-fin rays and mid-dorsal supratemporal pores in species of *Meiacanthus*.[1]

Species	Segmented anal-fin rays							Total pectoral-fin rays											Mid-dorsal supra-temporal pores	
	14	15	16	17	18	19	$\bar{x}$	24	25	26	27	28	29	30	31	32	33	$\bar{x}$	1	2
anema			42	153	56	1	17.1			10	15	213	8	5	1			27.9	3	210
ditrema		2	21	41	3		16.7			7	10	45	3	2				27.7	2	64
grammistes	27	111	29				15.0			2	2	61	26	65	5			29.0	105	1
kamoharai		5	5				15.5							10				30.0	9	
lineatus	1	34	33	5			15.6					3	4	59	5	4		30.0	53	
abditus		3	11*				15.8					10*	–	4				28.6	2	
limbatus				1			17.0					1						28.0	1	
crinitus	5*	6					14.6		1	10*								25.9	8	3
naevius		1					15.0		1									25.0	1	
geminatus	1	11	7	2			15.5	1	1	18	–	1						25.9	18	3
vicinus		1					15.0					1						28.0	1	
luteus		1	3	18*	9		17.1						1	12	4	13*	1	31.0	27	7
vittatus	3	15	6				15.1			20	3	1						26.2	23	
nigrolineatus	12	78	15				15.0	1	1	45	17	39	1	1				26.9	80	
mossambicus		6	16	3			15.9			1	1	20	2					28.0	24	
fraseri		11	16				15.6					22	3	2				28.3	27	
smithi		10	22	3			15.8			1	2	28	2	2				28.1	33	
atrodorsalis		24	127	80	5		16.3			2	5	158	27	44				28.4	85	1
ovalauensis			7	33	14		17.1				1	4	43	1	1			28.9	42	
tongaensis				7	11*		17.6					11	4*	3				28.6	18	
procne		11	12				15.5				1	21	1					28.0	23	
reticulatus				3	1		17.2					4						28.0	4	
bundoon			5	9			16.6						1	9	3	1		30.3	14	
phaeus				1			17.0									1		32.0	1	

[1] When counts vary, those for holotypes of new species are indicated by an asterisk.

TABLE 4. Frequency distributions of caudal-fin rays in species of *Meiacanthus*.[1]

Species	Total procurrent rays								Segmented rays				Total caudal-fin elements						
	8	9	10	11	12	13	14	$\bar{x}$	11	12	13	$\bar{x}$	20	21	22	23	24	25	$\bar{x}$
anema	18	29	63	6	3			9.6	5	9	98	12.8		73	43	83	3	1	22.1
ditrema			19	17	24			11.1	49			11.0		19	17	24			22.1
grammistes			9	20	85	15	3	11.8	125	7		11.1		7	25	96	16	3	22.9
kamoharai		1	1	2	1			10.6	3	4		11.6		2	—	3			22.2
lineatus	1	8	33	10	1			10.0	44	8	2	10.6	4	38	14	6			21.4
abditus			2					10.0	2			11.0		2					21.0
limbatus				1				11.0	1			11.0			1				22.0
crinitus			4*	4	3			10.9	9*	2		11.2		4*	3	3	1		22.1
naevius				1				11.0	1			11.0			1				22.0
geminatus	1	4	5	6				10.0	10	4	2	11.5	1	6	9				21.5
vicinus		1						9.0	1			11.0	1						20.0
luteus			2	2	20	4	2*	12.1	25*	4	1	11.2			2	20	6	2*	23.3
vittatus	1	9	7	3				9.6	9	7	4	11.7	2	10	8				21.3
nigrolineatus		11	30	29	12			10.5	56	23	4	11.4	4	32	36	22			21.8
mossambicus		1	2	9	8			11.2	13	6	1	11.4		1	6	13	1		22.7
fraseri			3	13	10			11.3	20	5	1	11.3		1	11	13	1		22.5
smithi		3	4	12	9	4		11.2	24	8	2	11.4		4	12	11	5	1	22.6
atrodorsalis		4	17	71	58	37	4	11.6	175	12	4	11.2	1	14	74	56	43	3	22.7
ovalauensis		2	4	21	11	4		11.3	44	3		11.1	1	4	24	10	4		22.3
tongaensis			4	5*	6	3		11.4	16*	2		11.1		4	5*	5	4		22.5
procne		1	7	11	1			10.6	18	2		11.1		7	12	1			21.7
reticulatus						4		13.0	4			11.0					4		24.0
bundoon			4	5	3	2		11.2	5	3	6	12.1			3	4	7		23.3
phaeus						1		13.0	1			11.0					1		24.0

[1] When counts vary, those for holotypes of new species are indicated by an asterisk.

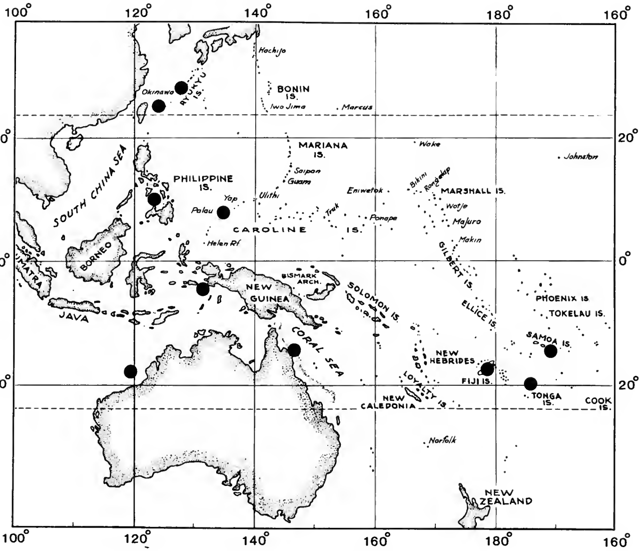


FIG. 5. Distribution of *Meiacanthus ditrema*.

depths of approximately 30 meters along drop-offs where small schools were observed swimming upside down in caves. Unfortunately no specimens of this *Meiacanthus* have yet been collected.

All of these species have allopatric distributions (Fig. 6), and are characterized by the combination of an essentially pale caudal fin and an adult color pattern consisting of two dark lateral body stripes in addition to one along the dorsal body contour. Because *M. anema*, sole member of the subgenus *Holomeiacanthus*, has multiple body stripes (but with ventral stripe indistinct in adult males), and multiple stripes also occur only in juveniles of some species of the subgenus *Meiacanthus*, the use of this color pattern character as a synapomorphy is problematical and the possibility exists that multiple stripes may be a primitive character state. Multiple body stripes also occur in three of ten species of species of *Petroscirtes*, the sister group of *Meiacanthus*.

Meiacanthus grammistes, whose distribution overlaps the total range of the *lineatus* species group, superficially resembles some of these species; however, it differs from all of them most obviously in having caudal-fin rays that are conspicuously spotted. *Meiacanthus lineatus* and *M. abditus* exhibit the greatest degree of

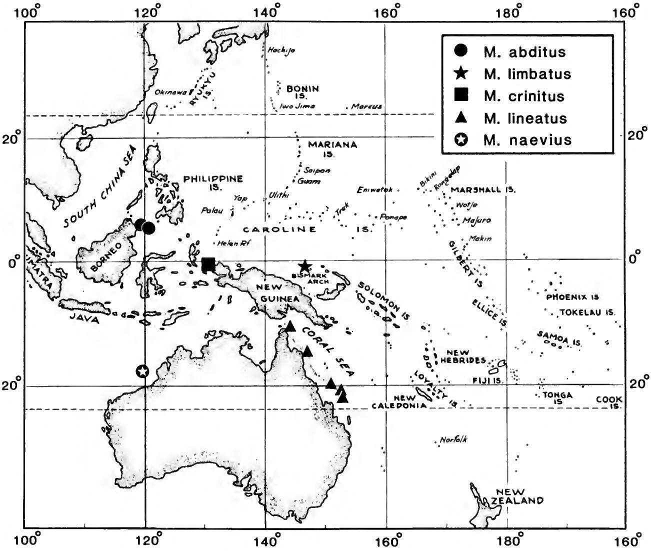


FIG. 6. Distribution of the *Meiacanthus lineatus* species group.

overall similarity and are contrasted in the following account.

Meiacanthus (Meiacanthus) abditus n. sp., Figs. 7b, 8b

Meiacanthus lineatus (non De Vis): Smith-Vaniz 1976: 90 (misidentification in part; Sulu Archipelago specimens).

DESCRIPTION. (See Tables 1–4 for frequencies of certain meristic characters.) Dorsal fin IV, 26 or 27. Anal fin II, 15 or 16. Pectoral fin 14. Caudal fin: procurrent rays 5 + 5; segmented rays 11. Vertebrae: precaudal 12 or 13; caudal 22 or 23; total 35 or 36. Pleural ribs on vertebrae 3–12 or 13; epipleural ribs 15–17. Incisor teeth in specimens 29–48 mm, n = 2: lower jaw 18–20; upper jaw 18. Lateral line terminates posteriorly below level of 5th or 6th segmented dorsal-fin ray; single mid-dorsal supratemporal pore (n = 2).

Sexual dimorphism probably as in *M. lineatus*, well developed in pelvic and caudal fins (Figs. 9–10) based on a single female 29.3 mm and male 48.3 mm; pelvic fin: male 25.7% SL, female 11.6% SL; longest outer caudal-fin lobe: male 41.8% SL, female 21.5% SL; longest inner caudal-fin ray: male 19.1% SL, female 20.8% SL. Outer lobes of caudal fin presumably elongated in adult males only, in-

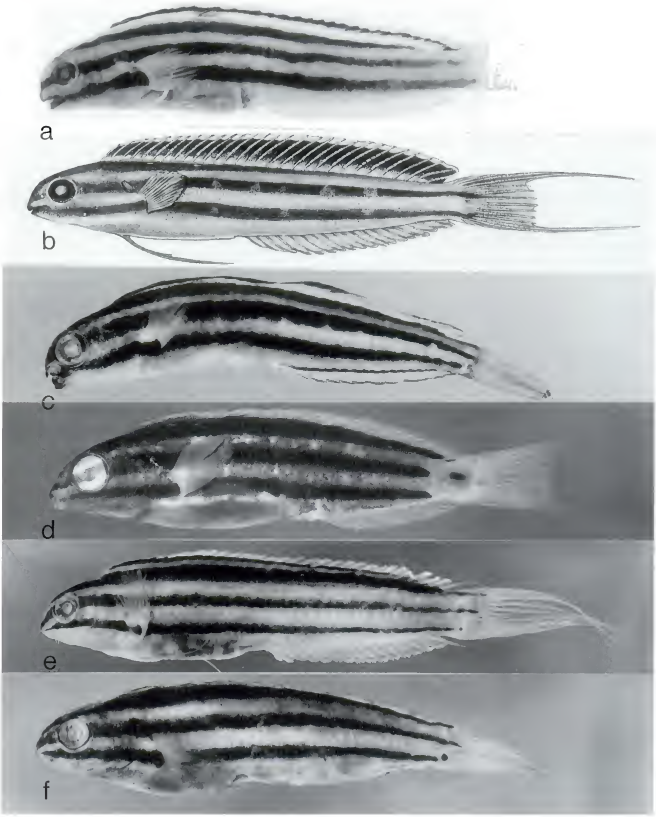


FIG. 7. *Meiacanthus* species. **a**, *M. lineatus,* USNM 201363, Australia, Great Barrier Reef, One Tree Is., male, 62.8 mm SL; **b**, *M. abditus,* USNM 99370, Sulu Archipelago, Sirun Is., male 48.3 mm (drawn by Mary H. Fuges); **c**, *M. limbatus,* holotype, WAM P.27826-018, Bismarck Archipelago, Manus Is., female, 37.0 mm; **d**, *M. naevius,* holotype, WAM P.28030-017, Western Australia, Rowley Shoals, female, 35.8 mm; **e**, *M. crinitus,* holotype, USNM 276512, Irian Jaya, male, 47.0 mm; **f**, *M. crinitus,* USNM 258768, Irian Jaya, female, 37.6 mm.

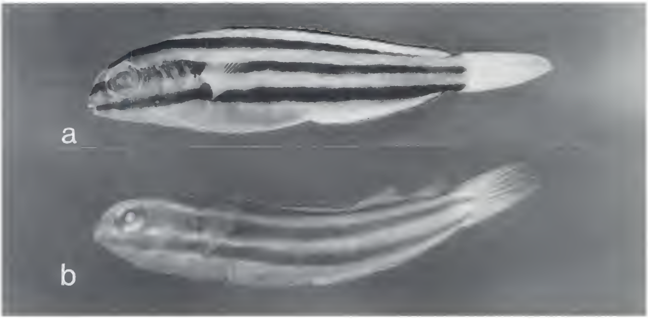


FIG. 8. Females of two closely related *Meiacanthus* species: a, *M. lineatus*, USNM 211308, Australia, Heron Is., 38.5 mm SL; b, *M. abditus*, holotype, USNM 276511, Sulu Archipelago, Jolo Is., 29.3 mm.

terradial membranes of inner rays slightly incised in large males.

COLOR PATTERN. Head and body have three dark stripes, separated by pale interspaces, extending the length of the body. The dorsalmost stripe, widest anteriorly, extends along the dorsal body contour to the end of the dorsal-fin base. The middle stripe extends from the margin of the upper lip through the eye, encroaches slightly onto the dorsal part of the pectoral-fin base, and terminates on the caudal fin. The ventral stripe extends from the lower jaw, beneath the eye, and through the lower half

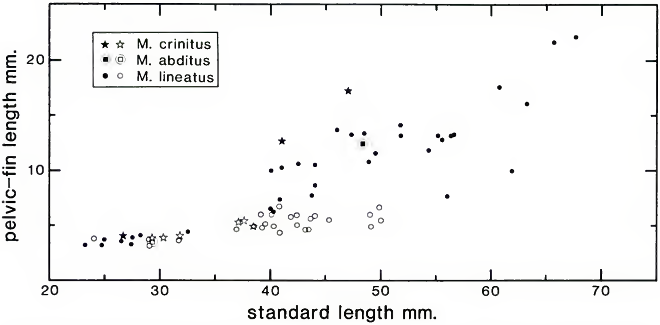


FIG. 9. Relationship between pelvic-fin length versus standard length in certain species of *Meiacanthus*. Closed symbols = males; open symbols = females.

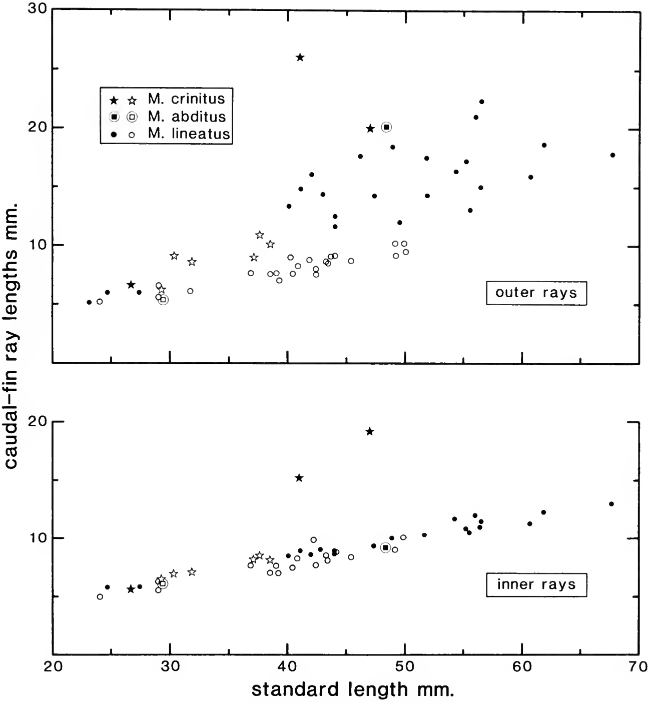


FIG. 10. Relationship between lengths of inner and outer caudal-fin rays versus standard length in certain species of *Meiacanthus*. Closed symbols = males; open symbols = females.

of the pectoral fin. Like the middle stripe, this stripe extends onto the proximal third of the caudal fin, where it tapers to a point. On the head a narrow, pale, predorsal interspace separates the dorsalmost stripe from its counterpart, except at the end where they join across the anterior interorbital region. The dorsal fin is pale proximally, followed by a dusky stripe with a narrow, pale border. In the single adult male, the dusky stripe extends the entire length of the dorsal fin and is about twice the width of the pale, proximal area of the fin. In the female holotype the width of this dusky stripe is about equal to the width of the anterior pale proximal area of the fin, but as it extends posteriorly the stripe becomes relatively narrower and fades completely before reaching the end of the fin. The other fins are pale, except for a pair of stripes that extend onto the caudal fin. Life color is unknown.

SPECIES COMPARISONS. A member of the *lineatus* species group (refer to discussion in previous account), *Meiacanthus abditus* can best be distinguished by its unique color pattern which most closely resembles that of *M. lineatus*. The primary color-pattern differences of these two species, with those of *M. abditus* given first, are as follows: dark snout stripe contacts margin of upper lip (versus separated by a pale area approximately equal width of stripe, Fig. 3b); dark middle and ventral body stripes distinctly extend onto caudal fin (versus one or both stripes typically terminating at base of caudal fin); and width of dark, submarginal dorsal-fin stripe at least as wide as pale proximal area of fin anteriorly (versus width of dark submarginal stripe distinctly narrower than anterior proximal area of fin).

ETYMOLOGY. The Latin "abditus," meaning hidden or concealed alludes to the previous confusion of this species with *M. lineatus*.

MATERIAL EXAMINED. Thirty specimens, 10.2–48.3 mm SL, all from Sulu Archipelago, Fig. 6.

Holotype. USNM 276511, female 29.3 mm SL, Sulu Archipelago, Jolo Island, Tutu Bay, 05°50′45″N, 120°01′15″E, dynamite in 3–6 m; 19 Sep 1909; "Albatross" sta. D.5561.

Paratypes. USNM 122384 (28, 10.2–14.1), same data as holotype; USNM 99370 (1, 48.3), Sirun Is., 05°35′40″N, 120°47′30″E; trawled in 31–38 m; 16 Feb 1908; "Albatross" sta. D.5148.

Meiacanthus (Meiacanthus) limbatus n. sp., Fig. 7c

DESCRIPTION. Dorsal fin IV, 26. Anal fin II, 17. Pectoral fin 14. Caudal fin: procurrent rays 5 + 6; segmented rays 11. Vertebrae: precaudal 13; caudal 22. Pleural ribs on vertebrae 3–13; epipleural ribs 14. Incisor teeth: lower jaw 14; upper jaw 13. Lateral line terminates posteriorly below level of 1st segmented dorsal-fin ray; pair of mid-dorsal supratemporal pores.

Sexual dimorphism unknown, female holotype only known specimen; pelvic fin 11.9% SL; outer lobes of caudal fin not elongated 20.0% SL; longest inner caudal-fin ray 18.9% SL. Interradial membranes of inner rays weakly incised.

COLOR PATTERN. Head and body have three dark stripes, which taper posteriorly and are separated by pale interspaces. The dorsalmost stripe extends along the dorsal body contour and terminates at the caudal-fin base dorsally. The middle stripe extends across the snout, through the eye, just above the pectoral fin, and terminates midlaterally at the caudal-fin base. The ventral stripe encircles the mouth, forming a broad band on the chin, extends through the lower half of the pectoral-fin base, and terminates on the caudal peduncle distinctly anterior to the caudal-fin base. The top of the head is dark except for a narrow predorsal stripe. Dorsal fin has narrow dark basal stripe, widest posteriorly, followed by a broad, pale area above which is a dark stripe (approximately half height of fin anteriorly but tapering to a narrow border posteriorly) with a minute pale distal margin. Anal fin is mostly pale except for a narrow, dark stripe at its base and a dusky distal margin. Pectoral, pelvic, and caudal fins are pale dusky. Life color is unknown.

SPECIES COMPARISONS. *Meiacanthus limbatus* differs from other members of the *lineatus* species group (see discussion under *M. lineatus*) most obviously in having a conspicuously dark chin (Fig. 3c) and an anal fin with a dark basal stripe.

ETYMOLOGY. The Latin "limbatus," meaning bordered, alludes to the dark stripe at the base of the anal fin.

MATERIAL EXAMINED. Holotype only known specimen.

Holotype. WAM P.27826-018, female 37.0 mm SL, Bismarck Archipelago, Manus Is., Los Negros I., 3 km E of aerodrome, 02°04'S, 147°25'E; 35–41 m; 6 Oct 1982; G. R. Allen and R. Knight.

Meiacanthus (Meiacanthus) naevius n. sp., Fig. 7d

DESCRIPTION. Dorsal fin IV, 26. Anal fin II, 15. Pectoral fin 12 or 13. Caudal fin: procurrent rays 6 + 5; segmented rays 11. Vertebrae: precaudal 14; caudal 20. Pleural ribs on vertebrae 3–14; epipleural ribs 15. Incisor teeth: lower jaw 23; upper jaw 22. Lateral line terminates posteriorly below level of 3rd (right side) or 5th (left side) segmented dorsal-fin ray; single mid-dorsal supratemporal pore.

Sexual dimorphism unknown, female holotype only known specimen; pelvic fin 14.0% SL; outer lobes of caudal fin slightly elongated 26.5% SL; longest inner caudal-fin ray 20.5% SL. Interradial membranes of inner rays weakly incised.

COLOR PATTERN. Head and body have three dark stripes, separated by dusky interspaces. The middle and ventral stripes both terminate distinctly in front of the caudal peduncle slightly anterior to the end of the anal fin. An elongate, dark spot on the caudal peduncle appears to be a disjunct piece of the middle stripe. The dorsalmost stripe, which is not well defined on the head, follows the dorsal body contour, narrows posteriorly, and terminates near the end of the dorsal fin. The middle stripe originates on the snout, crosses through the eye, and extends posteriorly just above the pectoral fin. The ventral stripe extends from the lower jaw, beneath the eye, and through the lower half of the pectoral fin. Dorsal fin has proximal two-thirds to one-third of fin dark, the pigmented area decreasing posteriorly; remainder of dorsal fin is pale, except for very narrow dark border. Anal fin is pale, except for faint, dusky border. The caudal fin is essentially pale with the rays faintly overlain with melanophores, and a scattering of large, dusky melanophores on the upper half of the fin proximally. Pectoral and pelvic fins are pale. Life color is unknown.

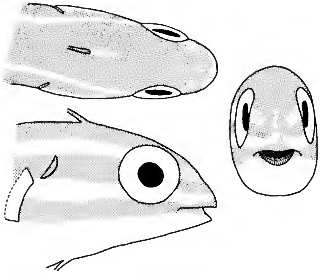


FIG. 11. Head color pattern of *Meiacanthus naevius*.

SPECIES COMPARISONS. *Meiacanthus naevius* differs from other members of the *lineatus* species group (see discussion under *M. lineatus*) most obviously in having an isolated, elongate spot on an otherwise unmarked caudal peduncle. Its dorsal fin pigmentation and head color pattern (Fig. 11) are also distinctive.

ETYMOLOGY. The Latin "naevius," meaning with a birthmark, alludes to the conspicuous spot on the caudal peduncle.

MATERIAL EXAMINED. Holotype only known specimen.

Holotype. WAM P.28030-017, female 35.8 mm SL, western Australia, Rowley Shoals, Clerke Reef, 2 km S Bedwell I., 17°18'S, 119°20'E; 3–5 m; 11 Aug 1983; G. R. Allen and R. Steene; sta. ROW 83-010.

Meiacanthus (Meiacanthus) crinitus n. sp., Figs. 7e–f

DESCRIPTION. (See Tables 1–4 for frequencies of certain meristic characters.) Dorsal fin IV (rarely III), 25 or 26. Anal fin II, 14 or 15. Pectoral fin 12 or 13 (typically 13). Caudal fin: procurrent rays 5–6 + 5–6

= 10–12; segmented rays 11 or 12. Vertebrae: precaudal 12–14; caudal 19–21; total 32–34. Pleural ribs on vertebrae 3–12 to 14; epipleural ribs 12–14. Incisor teeth in specimens 29–47 mm, n = 8: lower jaw 20–24; upper jaw 19–21. Lateral line terminates posteriorly below level of 5th or 6th segmented dorsal-fin ray; either single mid-dorsal supratemporal pore (n = 8) or pair of pores (n = 3).

Sexual dimorphism well developed in pelvic and caudal fins (Figs. 9–10) in 2 males 41–47 mm and 6 females 29.2–38.5 mm; pelvic fin: males 31.0–36.6% SL, females 12.5–14.4% SL; longest outer caudal-fin lobe: males 42.6–63.4% SL, females 24.3–30.0% SL; longest inner caudal-fin ray: males 37.1–40.9% SL, females 21.3–22.8% SL. Outer lobes and inner rays of caudal fin elongated in adult males only, interradial membranes of inner rays strongly incised in large males.

COLOR PATTERN. Head and body have three dark stripes, which taper posteriorly and are separated by pale interspaces. The dorsalmost stripe, widest anteriorly, extends along the dorsal body contour and terminates either on the dorsum of the caudal peduncle or extends onto the bases of the upper caudal-fin rays. The middle stripe extends from the upper lip, diagonally across the snout, through the eye, just above the pectoral fin, and terminates as a narrow line on the caudal-fin base. The ventral stripe extends from the side of the upper lip, to beneath the eye, and through the lower half of the pectoral fin; this stripe continues almost to the caudal-fin base, where it typically ends as a small, slightly separated spot. The top of the head is dark, except for a narrow predorsal stripe. In males, the dorsal fin is dark basally above which is a dusky stripe followed by a black submarginal stripe, which extends almost the entire length of the fin, and finally has a pale distal margin; the pale border of the fin is very narrow anteriorly but includes at least a third of the fin posteriorly. In females, the dorsal fin is dark basally above which is a pale submarginal stripe, widest posteriorly, extending the entire length of the fin, and capped with a narrow dark border. In both sexes the pale anal fin has a narrow dusky margin. The pectoral fin is pale with the rays delicately outlined with melanophores. The caudal fin is pale dusky except for the continuation of the dark body stripes onto the fin base. Life color is unknown.

SPECIES COMPARISONS. *Meiacanthus crinitus* differs from other members of the *lineatus* species group (see discussion under *M. lineatus*) in its unique pattern of stripes on the caudal-fin base and in having the inner caudal-fin rays greatly elongated and deeply incised in adult males. Within the *lineatus* group, only it and *M. naevius* have 12 or 13 pectoral-fin rays.

ETYMOLOGY. The Latin "crinitus," meaning hairy, with long hair alludes to the elongate inner caudal-fin rays which distinguish adult males of this species.

MATERIAL EXAMINED. Eleven specimens, 47.0–17.5 mm SL, all from West Irian, Fig. 6.

Holotype. USNM 276512, male 47.0 mm, New Guinea, NW tip of Irian Jaya, Batana Is., Marchesa Bay, Hawaii I., 0°49′48″S, 130°56′48″E; 0–6 m; 2 Jul 1979; B. B. Collette et al.; sta. BBC 1731.

Paratypes. ANSP 157993 (2, 31.8–37.1), USNM 258768 (7, 17.5–41.0), same data as holotype.

Meiacanthus grammistes (Valenciennes)

Observations and a color photograph (here reproduced in half-tone as Fig. 12) provided by Dr. Hitoshi Ida suggest that in the Philippines the cardinal fish *Cheilodipterus nigrotaeniatus* Smith and Radcliffe is a Batesian mimic of *Meiacanthus grammistes*. Both species have similar dark body stripes and spotted caudal fins, and further agree in having the anterodorsal region of the head and body yellow, the remaining pale areas white. Several *Cheilodipterus*, employing the same swimming

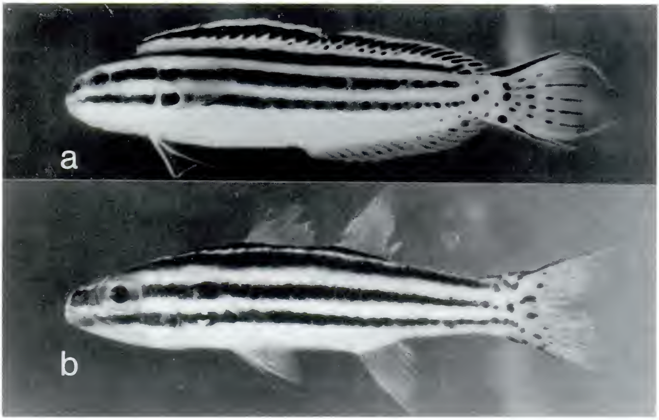


FIG. 12. Presumed mimetic species-pair. Above, *Meiacanthus grammistes*, 63 mm SL; Below, *Cheilodipterus nigrotaeniatus*, 74 mm SL. Both from the Philippines, Mindanao, Samal Island. Photographs courtesy of Hitoshi Ida.

behavior as that of a group of *M. grammistes*, were observed out in the open away from protective cover. A Batesian mimetic association involving *C. zonatus* Smith and Radcliffe and *M. vittatus* has previously been documented (Allen et al. 1975; Russell et al. 1976).

Meiacanthus geminatus Smith-Vaniz, Fig. 14a

A western Pacific endemic, *Meiacanthus geminatus* is known from Darvel Bay, Sabah (northwest Borneo), and Palawan Province, the Philippines. When orginally described *M. geminatus* was erroneously thought to consist of two widely disjunct populations based on two specimens from Darvel Bay and two badly faded examples from Australia. Because the Australian specimens (now shown to be a new species, *M. luteus*) had higher meristic values than the two Darvel Bay specimens they were not designated as types.

SPECIES COMPARISONS. *Meiacanthus geminatus* together with *vicinus*, *luteus*, and *vittatus* appear to comprise a closely related group that is unique within the subgenus *Meiacanthus* in having a single dark, lateral stripe, mostly positioned above the pectoral fin, in addition to one which may occur along the dorsal body contour. These four species, which are compared in Table 5, further agree in having pelvic and caudal fins that both exhibit a moderate degree of sexual dimorphism. Certain aspects of the lateral stripe pattern shared by *M. geminatus-vicinus* and *M. luteus-vittatus* suggest that they are geminate species-pairs. The allopatric distribution patterns of these species (Fig. 13) are compatible with such a hypothesis of relationships.

TABLE 5. Comparison of selected characters in members of the *Meiacanthus geminatus* species group.

Species	*M. geminatus*	*M. vicinus*	*M. luteus*	*M. vittatus*
Pectoral rays modally	13	14	15 or 16	13
Inner caudal rays elongated in adult males	no	no	no	yes
Color of body above lateral stripe	?	?	yellow	gray
Coloration of dorsal fin proximally	chestnut brown	black	pale brown	gray
Aspects of dark lateral stripe:				
encroachment onto pectoral-fin base	none	none	slight	moderate
position on caudal fin	distinctly below center	approximately centered	approximately centered	approximately centered
width on snout	narrow, Fig. 4a	narrow, Fig. 4b	wide, Fig. 4c	wide, Fig. 4d
in adult males dorsal margin anteriorly with white border	no	no	yes	yes

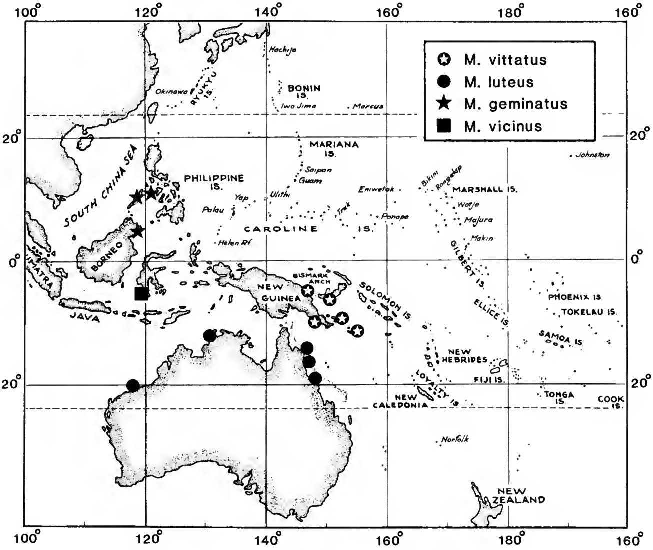


FIG. 13. Distribution of the *Meiacanthus geminatus* species group.

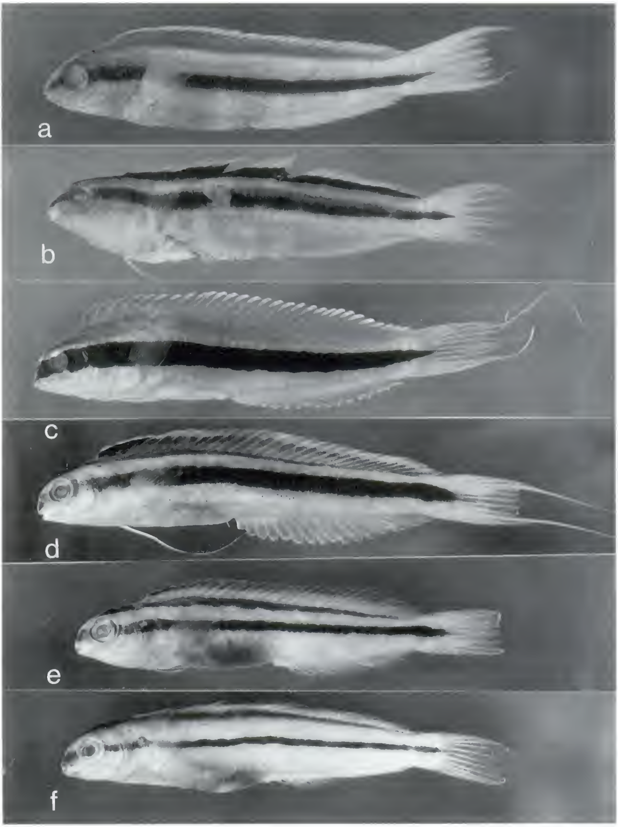


FIG. 14. *Meiacanthus* species. **a**, *M. geminatus*, USNM 218703, Philippines, Cuyo Is., female, 47.1 mm SL; **b**, *M. vicinus*, holotype, NTM S.10663-002, Sulawesi, male, 40.6 mm; **c**, *M. vittatus*, AMS I.20428-001, Papua New Guinea, Port Moresby, male, 44.2 mm; **d**, *M. luteus*, holotype, NTM S.11358-001, Australia, Darwin Harbor, male, 51.0 mm; **e**, *M. luteus*, NTM S.11358-002, Australia, Darwin Harbor, female, 39.2 mm; **f**, *M. luteus*, NTM S.11083-001, Australia, northwest shelf, female, 42.2 mm.

NEW MATERIAL. PHILIPPINES: Palawan Prov., Rita Is., 10°05′N, 118°47′E, BPBM 28703 (1, 31.0), USNM 220938 (1, 27.1); Cuyo Islands, 10°15′12″N, 121°00′14″E, USNM 218703 (15, 16.5–47.1); Cuyo Islands, 10°52′42″N, 120°56′44″E, USNM 222108 (2, 32.1–36.8).

Meiacanthus (Meiacanthus) vicinus n. sp., Fig. 14b

DESCRIPTION. Dorsal fin IV, 26. Anal fin II, 15. Pectoral fin 14. Caudal fin: procurrent rays 5 + 4; segmented rays 11. Vertebrae: precaudal 13; caudal 21. Pleural ribs on vertebrae 3–13; epipleural ribs 13. Incisor teeth: lower jaw 23; upper jaw 22. Lateral line terminates posteriorly below level of 5th–6th segmented dorsal-fin ray; single mid-dorsal supratemporal pore.

Sexual dimorphism probably as in *M. geminatus* (Figs. 15–16), male holotype only known specimen; pelvic fin 23.7% SL; outer lobes of caudal fin moderately elongated 34.2% SL; longest inner caudal-fin ray 23.9% SL. Interradial membranes of inner rays slightly incised.

COLOR PATTERN. The most distinctive feature of the color pattern is a dark midlateral stripe extending from snout through eye to center of caudal fin. The stripe, which is almost equal to the width of eye diameter at its widest point, completely envelopes the gill opening but does not extend onto the pectoral-fin base. On the postorbital region of head, the stripe is slightly wider than the pupil diameter, but becomes distinctly narrower as it extends onto the snout, where it is interrupted at the midline. The body is otherwise pale dusky, except for a blackish stripe that extends along its dorsal contour (scarcely visible in Fig. 14b) and continues onto the dorsal fin. This stripe, which gradually widens anteriorly, extends from the posterior third of the fin base to slightly beyond the interorbital region, where it then tapers to a point; on the head, a pale dusky interspace separates the dark stripe into a pair of counterparts. The entire basal half of the dorsal fin is black, with the distal half of the fin abruptly immaculate. The caudal fin is pale except for tapering dark stripe centered on proximal third of fin. Other fins are uniformly pale. Life color is unknown.

SPECIES COMPARISONS. As discussed in the previous account, *Meiacanthus vicinus* is a member of the *geminatus* species group and appears to be most closely related to *M. geminatus*. Only color pattern will distinguish these two species (see Table 5).

ETYMOLOGY. The Latin "vicinus," meaning near or neighboring, alludes to the presumed sister species relationship of this species and *M. geminatus*.

MATERIAL EXAMINED. Holotype only available specimen, although reported (B. C. Russell pers. comm.) to have been relatively common at the type locality.

Holotype. NTM S.10663-002, male 41.3 mm SL, Sulawesi, Barang Lompo, 12 km N of Udjung Pandang, 05°03′S, 119°20′E; 10 m; 13 Oct 1982; B. C. Russell; sta. BCR 82-5.

Meiacanthus (Meiacanthus) luteus n. sp., Figs. 14d–f

Meiacanthus geminatus (non Smith-Vaniz): Smith-Vaniz 1976: 95 (misidentification in part; Australian specimens).

DESCRIPTION. (See Tables 1–4 for frequencies of certain meristic characters.) Dorsal fin IV (rarely III), 25–27. Anal fin 15–18. Pectoral fin 14–17 (typically 15 or 16). Caudal fin: procurrent rays 5–7 + 5–7 = 10–14; segmented rays 11–13; total elements 22–25. Vertebrae: precaudal 12–14; caudal 22–24; total 35–37. Pleural ribs on vertebrae 3–12 to 14; epipleural ribs 12–15. Incisor teeth in specimens 34–67 mm, n = 20; lower jaw 20–25; upper jaw 17–24. Lateral line terminates posteriorly below level of 3rd to 7th segmented dorsal-fin ray; either single mid-dorsal supratemporal pore (n = 27) or pair of pores (n = 7).

Sexual dimorphism well developed in

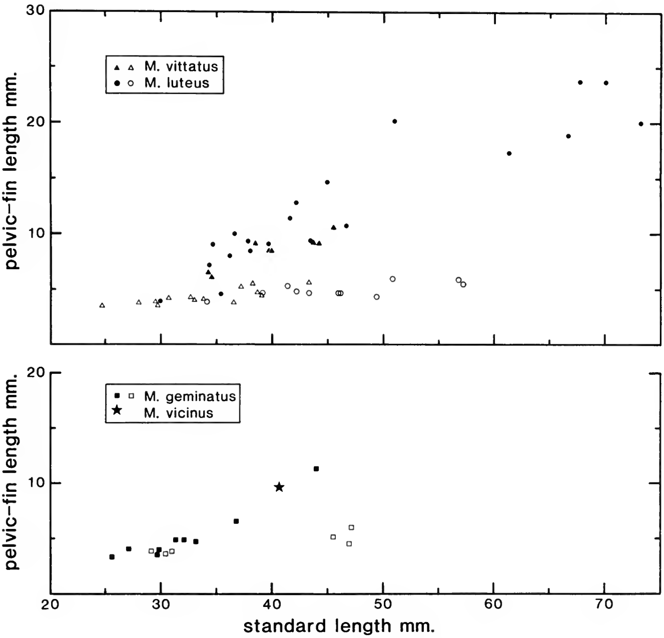


FIG. 15. Relationship between pelvic-fin length versus standard length in the *Meiacanthus geminatus* species group. Closed symbols = males; open symbols = females.

pelvic (Fig. 15) and caudal (Fig. 17) fins in 19 males, 34–73 mm and 11 females, 34–57 mm; pelvic fin: males 13.0–39.6% SL, females 8.9–12.8% SL; longest outer caudal-fin lobe: males 32.9–78.6% SL, females 21.0–26.8% SL; longest inner caudal fin ray: males 18.0–21.6% SL, females 17.8–21.7% SL. Outer lobes of caudal fin elongated in adult males only, interradial membranes of inner rays weakly incised (Fig. 18a).

COLOR PATTERN. The most distinctive feature of the color pattern is a dark midlateral stripe, which, in most specimens, is about half the width of the eye diameter, and extends from the snout to the center of caudal fin. This stripe is broadly continuous across the snout, completely envelopes the gill opening, and extends slightly onto the dorsal part of the pectoral-fin base. The body is otherwise pale dusky except for a brownish stripe along its dorsal

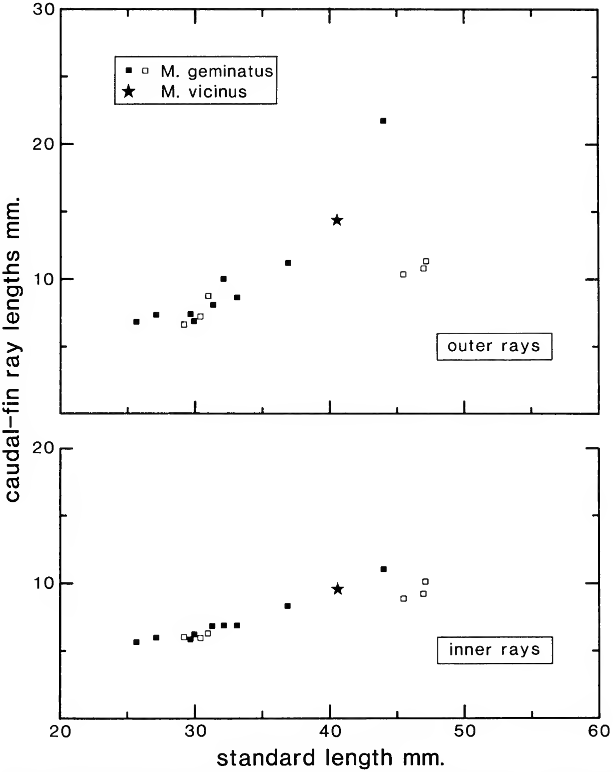


FIG. 16. Relationship between lengths of inner and outer caudal-fin rays versus standard length in *Meiacanthus geminatus* and *M. vicinus*. Closed symbols = males; open symbols = females.

contour that is widest anteriorly, extending from interorbital region to end of the dorsal fin. The top of the head is dark, except for a narrow predorsal stripe. In males the basal half to two-thirds of the dorsal fin is light dusky; the spinous part of the fin has a blackish submarginal area with a narrow white distal border, and the remainder of the fin is pale. The dorsal fin of females is mostly pale with a dusky margin, and is

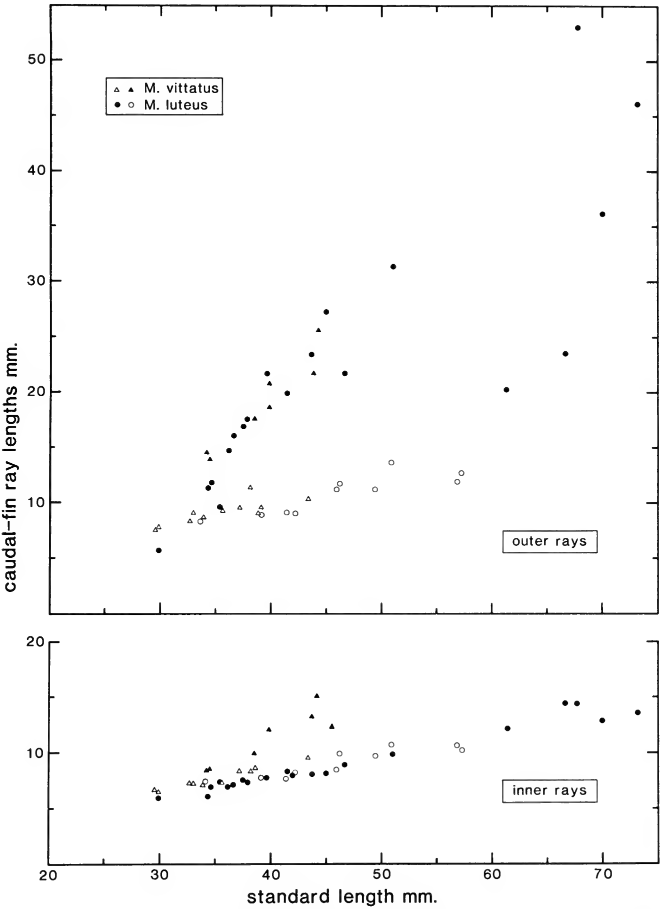


FIG. 17. Relationship between lengths of inner and outer caudal-fin rays versus standard length in *Meiacanthus vittatus* and *M. luteus*. Closed symbols = males; open symbols = females.

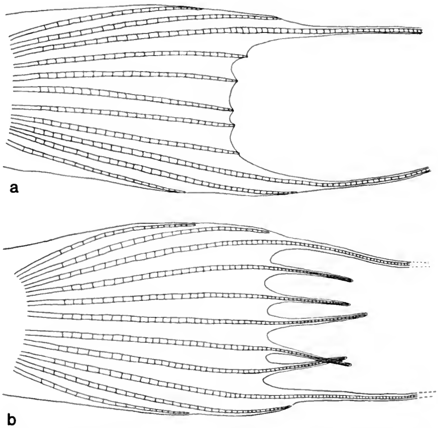


FIG. 18. Caudal fins of adult males in two species of *Meiacanthus* showing differences in degree to which inner rays are exerted beyond the margin of interradial membranes. **a,** *M. luteus,* AMS I.24785-001, 39.6 mm SL; **b,** *M. vittatus,* ANSP 126900, 43.7 mm.

darkest anteriorly. Caudal fin is pale except for short extension of the dark mid-lateral stripe onto central base of fin; stripe may continue farther onto fin as a diffuse sprinkling of melanophores. The other fins are unmarked. The single specimen available from the northwest shelf (Fig. 14f) has a dark lateral stripe that is narrower than that of specimens from other localities.

The life coloration of specimens from Darwin Harbor was as follows: mid-lateral stripe varying from brown to blackish with a narrow white dorsal border on postorbital region of head (males only); head and body below stripe whitish, brilliant yellow above, except for brownish stripe along dorsal body contour; in males, rayed portion of dorsal fin pale yellow distally with narrow white margin, in females pale dusky distally; anal fin pale yellow with narrow white margin (males) or mostly whitish (females).

SPECIES COMPARISONS. A member of the *geminatus* species group (see discussion under *M. geminatus*), *Meiacanthus luteus* can be distinguished by its color pattern and higher number of pectoral-fin rays.

ETYMOLOGY. The Latin "luteus," meaning yellow, refers to the brilliant upper body coloration of this species.

MATERIAL EXAMINED. Thirty-one specimens, 29.9–73.1 mm SL, all from Australia, Fig. 13.

Holotype. NTM S.11358-001, male 51.0, Australia, Darwin Harbor, reef by east arm boat ramp, 12°29′S, 130°53′E; 0.2–1 m; 29 Aug 1984; Helen A. Larson et al.; sta. HL 84-34.

Paratypes. DARWIN HARBOR: AMS I.24785-001 (4, 29.9–42.1), ANSP 153560 (3, 34.6–43.6), NTM S.11358-002 (2, 39.2–41.5), USNM 268915 (3, 36.6–46.6), same data as holotype; AMS IA. 6002 (1, 37.5), Mar 1934, F. R. Morris; AMS I.21964-002 (1, 34.3), 1979, T. Jackson; NTM S.11146-001 (1, 43.2), 19 Mar 1984, P. Alderslade. NORTHWEST SHELF: NTM S.11083-001 (1, 42.2), 20°9.4′S, 117°30.8′E–20°10.5′S, 117°32.2′E, trawled in 33–35 m, 18 Oct 1983, "Soela" cr. 5, sta 67. QUEENSLAND: QMB I. 10856 (1, 73.1), north Queensland coast, "Challenger Survey," 30 Oct 1957; QMB I.11117 (1, 53.1) off Cairns, K. Bryson; QMB I.18510 (2, 46.2–49.4), Green Is., 40 m, 9 Oct 1980. LIZARD IS. VICINITY: AMS I.20751-019 (1, 56.8), QMB I.16218 (1, 50.8), 14°38′S, 145°24′E, 25 m, 8 Feb 1979, sta FNQ 79–15; AMS I.20753-023 (1, 34.0), QMB I.15849 (1, 35.4), 14°36′S, 145°14′E, 14–15 m, 8 Feb 1979, sta FNQ 79–17; AMS I.20754-003 (1, 45.9), 14°33′S, 145°06′E, 16 m, 8 Feb 1979, sta FNQ 79–18. NORTH PALM IS.: QMB I.11059 (2, 57.2–66.6), 18°33′S, 146°30′E, G. Coates. TOWNSVILLE VICINITY: AMS I.26855-001 (1, 61.3); ANSP 153559 (1, 70.0), 18°55′S, 147°06′E, 29–32 m, 8 May 1977, A. Birtles.

Meiacanthus nigrolineatus Smith-Vaniz, Fig. 19

This relatively common species was previously known from the Gulfs of Suez and Aqaba, and an apparently disjunct southern Red Sea population distinguished by a more melanistic color pattern. The new records listed below fill in the distributional gap and slightly extend the southern range of the species. The color pattern of Jiddah specimens (Fig. 19) is, as might be expected, intermediate compared to northern and southern Red Sea specimens.

Springer and Smith-Vaniz (1972) gave a detailed account of a mimetic trio consisting of *Meiacanthus nigrolineatus, Ecsenius graveri* (Pellegrin), and *Plagiotremus townsendi* (Regan). They were unaware of the following case of "school-oriented mimicry" reported by Dafni and Diamant (1984) involving juveniles of *M. nigrolineatus*. In the Gulf of Aqaba small schools of 10 to 100 juvenile cardinal fishes (Apogonidae) shelter among the spines of sea urchins, *Diadema setosum* (Leskel). Two or three juvenile *Meiacanthus nigrolineatus* (>10 mm TL) often aggregate with such cardinal fish schools. At this size the juvenile blennies are very similar in appearance to juvenile cardinal fishes, especially *Cheilodipterus bipunctatus* (Lachner), *C. lachneri* Klausewitz, and *Apogon* spp., which are all characterized by a color pattern consisting of dark body stripes on a pale background and a dark basicaudal spot on the caudal peduncle. The juvenile *Meiacanthus* color pattern persists until they attain 25–30 mm TL, at which length they develop a dissimilar adult color pattern and gradually decrease their association with juvenile cardinal fishes. The more abundant juvenile cardinal fishes apparently serve as mimetic models; their schooling behavior and striped color pattern are believed to have a confusing effect on predators and thus enhance survival of individuals. In this particular case, the juvenile *Meiacanthus* mimic may also contribute directly to the success of the model's survival by its deterrent venomosity.

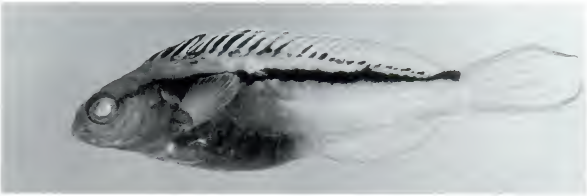


FIG. 19. *Meiacanthus nigrolineatus*, USNM 217726, Red Sea, Jeddah Harbor, female, 41.5 mm SL.

Because the adults of *M. nigrolineatus* have an aposematic color pattern and appear to be highly immune to predation, Dafni and Diamant (1984) asked the following question. Why do the juveniles have a totally different color pattern? They answered this question by suggesting the following possible benefit obtained by having dissimilar juvenile and adult color patterns. Being more vulnerable to predation, at least during the first encounter with a predator (as shown in their experiments), adoption of the adult color pattern by the less venomous juveniles would, conceivably, reduce its warning effectiveness. In this case school-oriented mimicry might serve as an attractive alternative that would enhance species survival.

Although the suggested benefit obtained by such mutual resemblance may indeed be real, no underlying evolutionary processes need be involved and the "mimetic" association may only be coincidental. A basicaudal spot and striped color pattern is not unique to juveniles of *M. nigrolineatus* and is perhaps characteristic [? plesiomorphic character state] of juveniles of most species of *Meiacanthus*. The primary motive force driving these juvenile blennies to form mixed schools with young cardinal fishes may be nothing more than shared exploitation of a shelter resource (i.e. long-spined sea urchins). As noted by Dafni and Diamant (1984), it would be interesting to know if juveniles of other species of *Meiacanthus*, in other parts of the Indo-Pacific region show similar relations with cardinal fishes.

NEW MATERIAL. SAUDI ARABIA: Jiddah Harbor, USNM 217726 (2, 41.5–52.9), USNM 217729 (2, 45.7–48.2). DJIBOUTI: Gulf of Tadjoura, USNM 278809 (1, 58.1), J. M. Rose pers. coll. 408-28 (1, 49.8).

Meiacanthus smithi Klausewitz

Although *Meiacanthus smithi* is easily distinguished from members of the *M. atrodorsalis* complex by its lack of an axillary pectoral spot and in having, in adults, sexual dimorphism well developed in the pelvic fins and absent in the caudal fin, it appears to be the likely candidate as the sister species of that group. *M. smithi* and *M. atrodorsalis* (at least some populations) are the only species of *Meiacanthus* that have a dark bar, sometimes incompletely developed on one or both sides, that extends from the posterodorsal margin of each orbit to the dorsal-fin origin. It is more parsimonious to assume that postorbital bars were present in a common ancestor shared by both *M. smithi* and the form that gave rise to the *M. atrodorsalis* complex than to assume that such a unique marking evolved independently. Remnant postorbital bars are present in some individuals of *M. tongaensis*, and their absence in *M. ovalauensis* is almost certainly a secondary development. That *M. smithi* and members of the *M. atrodorsalis* complex have adjacent but non-overlapping distributions may perhaps also be a reflection of their common ancestry.

THE *MEIACANTHUS ATRODORSALIS* COMPLEX

All members of the *Meiacanthus atrodorsalis* complex have identical or broadly overlapping meristic values (see Table 7). They also agree in having short, non-sexually dimorphic pelvic fins (8.4–16.2% SL), and caudal fins with outer lobes that are elongated and moderately sexually dimorphic (Figs. 21–22). They are further distinguished by the combination of an unstriped body and the presence of a dark spot on the ventral half of the pectoral-fin axil. This unique spot, which is normally hidden from view by the fin, is conspicuous when exposed (Smith-Vaniz 1976, Figs. 154–155) suggesting that it may play an important role in courtship and/or species recognition, and is considered to be a synapomorphy of the group. (See also discussion of relationships in preceding account of *Meiacanthus smithi*.) Species of *Meiacanthus* in which the adults have several body stripes, including one that extends through the ventral half of the pectoral fin, typically have a concentration of pigment in the pectoral-fin axil that is suggestive of the isolated spot characteristic of the *M. atrodorsalis* complex. Striped juveniles occur in several species of *Meiacanthus* (e.g. *M. smithi* and *mossambicus*) that as adults are unstriped and do not exhibit any trace of an axillary spot. The smallest available juvenile *M. atrodorsalis* (CAS 58011, 13.3 mm SL) is unstriped.

Only color pattern will distinguish the three species of the *Meiacanthus atrodorsalis* complex, which are briefly compared in Table 6. In view of the geographically isolated allopatric distributions (Fig. 20) of *Meiacanthus atrodorsalis*, *M. ovalauensis*, and *M. tongaensis* and their obviously close relationship, whether to recognize the trio as species or subspecies is a subjective decision. In recognizing them as full species I have been influenced by two considerations: (1) nomenclatural consistency —four allopatric, *Meiacanthus* species-pairs (*M. mossambicus–fraseri*, *M. grammistes–kamoharai*, *M. lineatus–abditus*, *M. geminatus–vicinus*) are recognized that are also distinguished primarily or solely on the basis of color pattern; and (2) full specific recognition will, in my opinion, more effectively call to the attention of other workers the existence of these forms, and perhaps stimulate them to search for additional characters upon which to re-evaluate their taxonomic status. The most important objective is to accurately and objectively describe these forms so that others will be aware of the situation.

Complex geotectonic processes associated with movements of the Indian-Australian and Pacific plates in the contact zone extending from the New Hebrides to the Tonga Islands have produced vicariant events that provide a speciation mechanism that could account for the distribution patterns exhibited by members of the *M. atrodorsalis* complex in that region. The Fiji Archipelago lies on a triangular piece of oceanic crust bounded by three trenches, past or currently active subduction zones (to the north the Vitiaz Trench, to the west the New Hebrides Trench, and to the southeast the Tonga Trench), and is considered to constitute a separate "Fiji Plate" (Robinson 1975). The separation of Fiji and the New Hebrides Islands is believed to have begun 6–8 m.y. ago and that of Fiji and the Tonga Islands about 5 m.y. ago (Kroenke 1984). Although Rotuma (12°30'S, 177°30'E) is presently somewhat geographically isolated, during the lowered sea levels of the last glaciation (20,000 years ago) it was part of a bridging Pacific Plate archipelago between the Santa Cruz Islands and Samoa that may have functioned as a west-east dispersal conduit (Robinson 1975).

Meiacanthus atrodorsalis Günther, Figs. 23a–f, 24a–d

Petroscirtes atrodorsalis Günther 1877: 198, pl. 115, Fig. B (orig. descr.; Samoa; holotype BMNH 1876.5.1.37).

Petroscirtes herlihyi Fowler 1946: 183, Fig. 47 (orig. descr.; Aguni Shima, Ryukyu Islands; holotype ANSP 72053).

As discussed above, the taxonomic status of members of the *M. atrodorsalis* complex is subjective and it could be argued that some or all of the five color pattern types here assigned to *atrodorsalis* should be recognized nomenclaturally. If future research reveals this to be the case, then the name *M. herlihyi* Fowler is available for type 1 morphs and the nominal name must be reserved for type 3 morphs at least. My decision to recognize all of these forms as one polytypic species is influenced by the fact that no two occur sympatrically (but see below), life coloration is inadequately known, and apparent differences in color patterns are relatively slight with some specimens difficult or impossible to categorize without knowledge of capture locality. There are large distributional gaps in the Moluccas islands region where morph types 2 and 3 might reasonably be expected to co-occur. Collections and observations of *M. atrodorsalis* from that area, especially near Ceram, hold the greatest promise of shedding additional light on the uncertain taxonomic status of these two forms. According to Milsom and Audley-Charles (1986), the Banda Arc is a separate tectonic unit that encloses the Banda Sea on three sides and includes Ceram at its northern end. The nearly sympatric occurrence of both type 2 and 3 morphs in the vicinity of Piru Bay, Ceram (see Fig. 20 insert) may indicate a recently established contact zone. One of the two specimens of type 3 morphs obtained from Piru Bay is shown in Fig. 23e.

The following remarks and references to published color photographs are intended to supplement the information given in Table 6. Locality records for type 2 morphs for which no specimens are available are also reported.

Morph 1: Body of adults is bicolored and all available specimens, including both sexes, have a relatively intense but incomplete dorsal-fin stripe. They also differ from type 2 morphs in having modally higher meristic values, especially total vertebrae. Color photographs have been published of an adult (Burgess and Axelrod 1972: fig. 286) and juvenile (Masuda et al. 1984: fig. 265-M).

Morph 2: Body is uniformly pigmented or very weakly bicolored, and dorsal fin is sexually dichromic; males have an incomplete dark stripe anteriorly which, if present, is less well developed in females. No color photographs of this morph have been published. Kodachrome slides taken by John E. Randall of a living individual from Banda Island show the following: body pale blue-gray anteriorly grading to very pale yellow posteriorly. Almost complete postorbital stripe present. Dorsal fin uniformly bright yellow except for incomplete, narrow dusky stripe anteriorly; caudal-fin lobes pale yellow. Slides taken by Rudie H. Kuiter of living individuals from Bali and Flores Island reveal their life coloration to be essentially identical to that of Banda specimens. According to V. G. Springer (pers. comm.), specimens from Kabaena Island, Sulawesi, were relatively uniformly pigmented and in life appeared whitish or pale blue-gray; they were collected and seen over pale bottom, which might have influenced their coloration.

The northernmost Philippine record plotted on the distribution map (Fig. 20) is based on a recent sight record of a typical type 2 morph observed by me at Duvuck Bay, Sabtang Island (20°18′N, 121°51′E). Another Philippine record is based on a Kodachrome slide, taken by E. O. Murdy, of a 42 mm SL (? female) postmortem specimen collected off Cape Bolinao. This individual had a uniform brown body with a concentration of melanophores on the dorsal and ventral margins of the caudal peduncle, and a narrow postorbital stripe. The dorsal fin was dusky yellow except for a dark basal blotch anteriorly that extended to the third spine. The caudal fin lobes were yellow without dusky margins.

Morph 3: This widely distributed morph exhibits no apparent sexual dichromatism and is characterized by an intense black dorsal-fin stripe through the middle of the fin that is essentially complete. The body is usually bicolored; in life it is blue-gray anteriorly gradually changing to yellow posteriorly. The elongate outer lobes of the caudal fin are also yellow. At least some individuals from most localities have a dark postorbital stripe (in life with a narrow pale blue or white border) on each side that fre-

TABLE 6. Comparison of certain aspects of the color pattern in members of the *Meiacanthus atrodrosalis* complex.

Recognized species and color morphs	Body color in life	Dark or contrasting dorsal-fin stripe	Postorbital stripe	Caudal peduncle blotches	Caudal fin lobes
M. atrodorsalis					
morph 1 (Fig. 23a)	blue-gray anteriorly becoming pale yellow, posteriorly	*both sexes:* with short black stripe; restricted to anterior ¼ to ⅓ of fin	present, but may be incomplete	absent	pale
morph 2 (Figs. 23b–d)	usually uniformly pigmented, varying from pale blue-gray to brownish; or body weakly bicolored, pale blue-gray anteriorly grading to pale yellow posteriorly	*females:* usually absent, large specimens occasionally with short, dusky stripe; *males:* narrow dusky stripe restricted to anterior ⅓ of fin	narrow and complete to incomplete or absent	usually present in large adults	pale or dusky
morph 3 (Figs. 23e–f)	variable, usually blue-gray anteriorly becoming pale yellow posteriorly; sometimes uniformly brownish	*both sexes:* with well-developed black stripe, typically complete (only 75–95% complete in Palau specimens)	prominent and complete to incomplete or absent	usually absent	pale or dusky
morph 4 (Figs. 24a–b)	unknown; preserved specimens uniformly pigmented or paler posteriorly	*both sexes:* fin uniformly brownish, darker anteriorly, especially in large males	absent	absent	pale
morph 5 (Figs. 24c–d)	blue-gray anteriorly becoming pale yellow posteriorly	*females:* large specimens with incomplete, dusky stripe; small specimens with fin uniformly brownish; *males:* black stripe on anterior ⅔ of fin, becoming brown and diffuse or absent posteriorly	usually absent; if present faint and incomplete	absent	pale
M. ovalauensis (Fig. 24e)	bright yellow; dorsum of head sometimes olive in large individuals	absent	absent	absent	pale; lobes of large adults may have narrow, dark border
M. tongaensis (Fig. 24f)	bright yellow-green	present and uniformly dark; typically complete; restricted to basal ½ to ¾ of fin.	absent or remnant	absent	pale; lobes of large adults may have narrow, dark border.

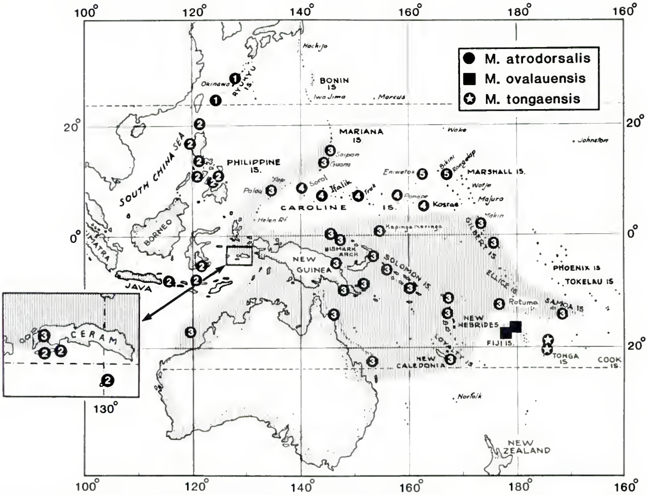


FIG. 20. Distribution of the *Meiacanthus atrodorsalis* complex. Shaded area indicates approximate distribution of the morph for which the name *atrodorsalis sensu stricto* applies; the 5 color pattern morphs (1–5) of *M. atrodorsalis* are indicated.

quently extends to the dorsal-fin origin. The intensity and completeness of this stripe is highly variable; specimens with and without the stripe may occur in the same collection. Specimens from at least New Guinea, Bismarck Archipelago, Solomon Islands, and Kapingamaringa Atoll have caudal fin lobes that are notably dusky. Occasional museum specimens have bodies that are uniformly pigmented. A color photograph of one such specimen, a 40.5 mm male from Marau, Solomon Islands (USNM 212032), appears in Burgess and Axelrod (1975: fig. 377). It is questionable whether the uniform brown body coloration of this postmortem photographed specimen accurately depicts its life colors. Published color photographs of more typically pigmented type 3 morphs are those of Burgess and Axelrod (1967: fig. 382) and Amesbury and Myers (1982: unnumbered fig.), based on living adults from the Great Barrier Reef and Guam, respectively. I have also examined unpublished color slides of typical specimens from the Coral Sea (Osprey Reef), Palau and Rotuma.

Morph 4: At least in preservation this morph has a color pattern that is most similar to type 2 morphs; indeed, it would be impossible to correctly assign some females. The primary pigmentary difference is that the dorsal fins of type 4 males have a broader and more diffuse concentration of melanophores. A recently collected 49.2

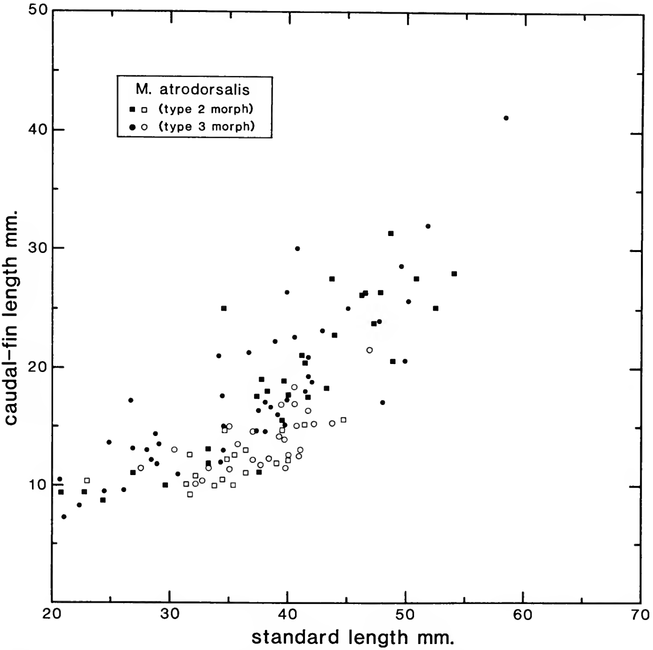


FIG. 21. Relationship between caudal-fin length versus standard length in two parapatric color morphs of *Meiacanthus atrodorsalis*. Closed symbols = males; open symbols = females.

mm Ponape male (USNM 223223) has a dorsal fin that is almost completely black anteriorly. No color observations are available.

Morph 5: The color pattern of this morph is somewhat intermediate compared to that of the two geographically nearest morphs, types 3 and 4. The posteriorly diffuse and usually incomplete dorsal-fin stripe clearly distinguishes this morph from type 3 morphs. Small females appear to be indistinguishable from type 4 morphs, but the dorsal-fin stripe is better developed in the adults of both sexes. Burgess and Axelrod (1971: fig. 373) give a color photograph of an Eniwetok adult and J. E. Randall has sent me unpublished slides of living adults from the same locality. These photographs agree with the observations of Losey (1972) who reported that in adults

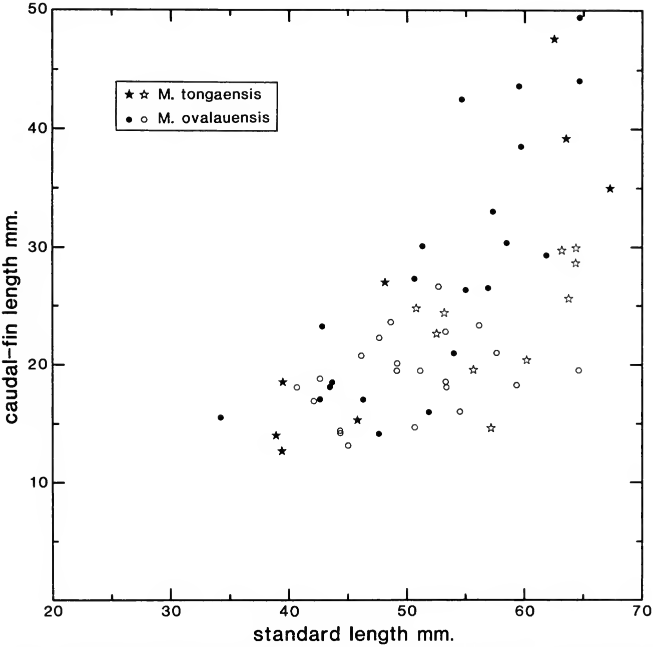


FIG. 22. Relationship between caudal-fin length versus standard length in *Meiacanthus ovalauensis* and *M. tongaensis*. Closed symbols = males; open symbols = females.

the caudal fin and posterior 29–49% of the body are bright yellow, with the remainder of the body blue-gray.

MATERIAL EXAMINED. (Asterisk denotes previously unexamined specimens.)

(Morph 1) RYUKYU IS.: Aguni Shimi, ANSP 72053 (23.8, holotype of *Petroscirtes herlihyi* Fowler), ANSP 72054-6 (3, 19.2–22.5); Ishigaki I., ANSP 128831 (1, 34.5), BPBM 7458 (1, 54.5), BPBM 7461 (2, 47.9–56.7).

(Morph 2) PHILIPPINES: Batangas, Caban Is., *USNM 228927 (1, 24.4); Palawan Province, Cocoro Is., *USNM 263303 (1, 41.4); Cebu, *USNM 263298 (1, 43.9); Mactan Is., *USNM 263301 (3, 37.7–43.2); Balicasag Is., *ANSP 152371 (4, 26.9–46.2), *USNM 263307 (3, 22.6–40.1); Mindanao, Zamboanga del Norte, *USNM 225123 (1, 20.5), *USNM 263300 (2, 29.6–40.2), *USNM 263304 (2, 47.8–54.0), *USNM 263305 (4, 23.0–41.4); Negros Oriental, *ANSP 152369 (2, 46.5–47.2), *USNM 225128 (1, 44.7), *USNM 263302 (3, 18.9–52.5), *USNM 263306 (4,

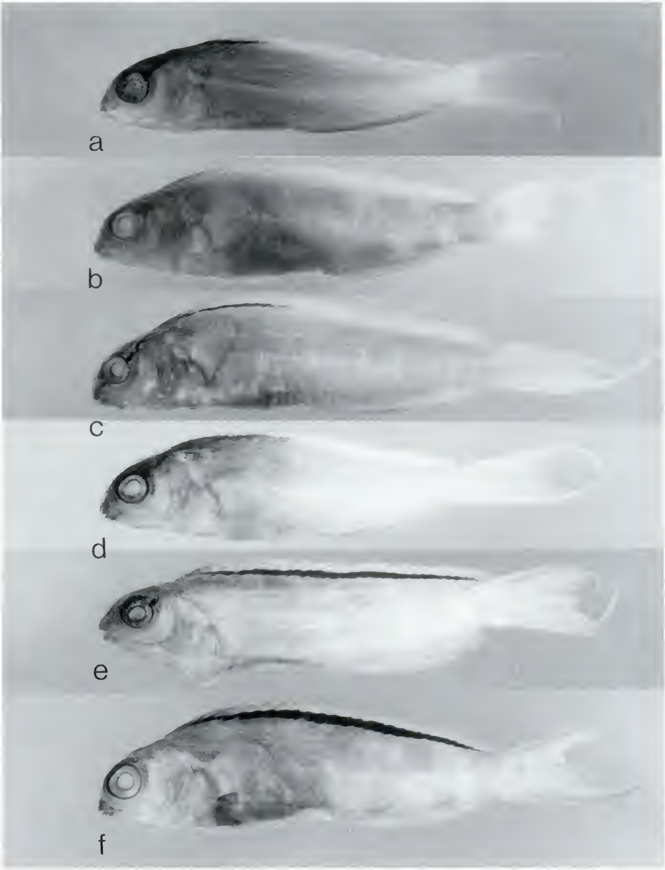


FIG. 23. *Meiacanthus atrodorsalis*. **a**, ANSP 128831, Ryukyu Is., male, 34.5 mm SL; **b**, USNM 263306, Philippines, Negros Oriental, female, 39.5 mm; **c**, ANSP 152371, Philippines, Balicasag Is., male, 46.2 mm; **d**, USNM 211938, Banda Is., female, 34.6 mm; **e**, USNM 209710, Ceram, Piru Bay, male, 39.2 mm; **f**, ANSP 152372, Papua New Guinea, Ninigo Is., female, 37.4 mm.

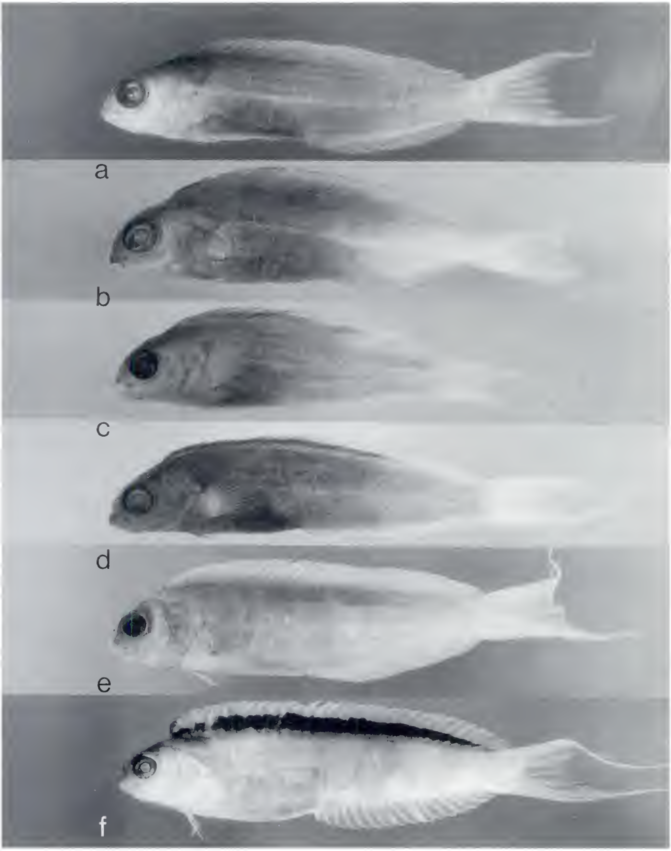


FIG. 24. *Meiacanthus* species. **a**, *M. atrodorsalis*, CAS 28904, Ifalik Atoll, female, 40.9 mm SL; **b**, *M. atrodorsalis*, USNM 223223, Ponape, female, 43.4 mm; **c**, *M. atrodorsalis*, USNM 142222, Marshall Is., Rongelap, female, 35.6 mm; **d**, *M. atrodorsalis*, USNM 201490, Marshall Is., Taka, male, 43.6 mm; **e**, *M. ovalauensis*, USNM 236031, Fiji Is., Ono-i-lau, female 56.2 mm SL; **f**, *M. tongaensis*, holotype, BPBM 30877, Tonga Is., Tongatapu, male, 62.5 mm.

TABLE 7. Geographic variation in frequency distributions of certain meristic characters in members of the *Meiacanthus atrodorsalis* complex.

Recognized species and color morphs	Total vertebrae						Total dorsal-fin elements					Segmented Anal-fin rays					Total pectoral-fin rays						
	33	34	35	36	37	$\bar{x}$	29	30	31	32	$\bar{x}$	15	16	17	18	$\bar{x}$	26	27	28	29	30	31	$\bar{x}$
M. atrodorsalis (morph 1)																							
Ryukyu Is.			2	5	1	35.9		3	4	1	30.8		4	3	1	16.6			1	–	7		29.8
M. atrodorsalis (morph 2)																							
Philippines	7	24	4			33.9	15	20			29.6	10	24	1		15.7			30	2	3		28.2
Sulawesi	3	6	1			33.8	5	5			29.5	4	5	1		15.7			10				28.0
Banda Sea	1	4	2			34.1	3	4			29.6	1	6			15.9			6	1			28.1
Longley Collection (Banda Sea[1])		1				34.0		1			30.0		1			16.0			1				28.0
M. atrodorsalis (morph 3)																							
Mariana Is.	1	1	12	1		34.9		8	6	1	30.5		8	7		16.5			5	2	8		29.2
Palau		2	4	2		35.0		5	3		30.4		6	2		16.2			7	1			28.1
Ceram		2				34.0		2			30.0	1	1			15.5		1	1				27.5
New Guinea-Bismarck Arch.	2	13	5			34.2	6	13	1		29.8	2	19	11		16.3			18	6	8		28.7
Kapingamaringa		9	15			34.6	2	18	4		30.1	2	15	7		16.2		2	18	2	2		28.2
Solomon Is.		2	2			34.5	1	1	2		30.2		2	2		16.5	1	–	3				27.5
E. Australia		2	3			34.6		4	2		30.3		6			16.0			6				28.0
New Caledonia		3	4	1		34.8		4	2	2	30.8		5	2	1	16.5			7	1			28.1

Santa Cruz–New Hebrides Is.	3	2			34.4	1	4			29.8	1	2	2		16.2			3	1	1		28.6
Rotuma	3	8	1		34.8		8	4		30.3		7	5		16.4					11	1	30.1
Samoa	1	1	1		35.0		1	2		30.7		2	1		16.3			1	–	2		29.3
Longley Collection (Samoa[1])		7			35.0		2	5		30.7		1	6		16.9					7		30.0
Gilbert Is.		6			35.0			6		31.0			6		17.0			2	2	2		29.0
M. atrodorsalis (morph 4)																						
Sorol-Ifalik	1	5	3	1	35.4		4	4	2	30.8		1	8	1	17.0			5	3	2		28.7
Truk	1	4	2		35.1		3	3	1	30.7	1	2	4		16.4			5	1	1		28.4
Ponape	3	13	4		35.1		4	9	7	31.2	2	12	6		16.2	1	–	15	3	1		28.2
Kosrae		3			35.0		1	2		30.7		1	2		16.7			3				28.0
M. atrodorsalis (morph 5)																						
Marshall Is.		10	5	1	35.4		3	12	1	30.9		4	10	2	16.9		2	10	2	2		28.2
M. ovalauensis																						
Fiji Is.	3	28	19	2	35.4		6	38	10	31.1		7	33	14	17.1		1	4	43	1	1	28.9
M. tongaensis																						
Tongatapu		2	9		35.8			3	8	31.7			4	7	17.6			7	2	2		28.5
Neiafu		1	6		35.9			4	3	31.4			3	4	17.6			4	2	1		28.6

---

[1] Refer to footnote in material examined section under account of *M. atrodorsalis* for discussion of the probable geographic origin of Longley's specimens.

33.2–48.6), *USNM 263310 (1, 48.8), *USNM 263311 (1, 39.0), *USNM 263312 (1, 50.8). SULAWESI (= CELEBES): Kabaena Is., USNM 211902 (1, 37.6), USNM 211912 (9, 20.7–35.4). BANDA SEA: Ambon Is., USNM 211952 (2, 27.4–31.0); Saparua Is., USNM 210141 (1, 22.8); Banda Is., USNM 211931 (1, 43.6), USNM 211938 (1, 34.6), USNM 211942 (1, 38.2), USNM 211943 (1, 32.2); Longley Collection (presumably from Banda Sea[1]), *USNM 277601 (1, 41.4).

(Morph 3) MARIANA IS.: Saipan, UG 5106 (3, 42.0–58.6); Tinian, UG 5175 (2, 37.0–41.1); Guam, *BPBM 7462 (1, 30.0), CAS 28920 (1, 19.0), UG 4243 (1, 43.0), UG 4322 (7, 39.9–46.7). PALAU IS.: ANSP 124873 (1, 42.4), BPBM 9635 (1, 58.6), *BPBM 9972 (1, 17.7), CAS 28918 (2, 30.7–33.7), CAS 28919 (3, 36.0–45.0). BANDA SEA: Ceram, Piru Bay, USNM 209710 (1, 39.2), USNM 209843 (1, 28.8). NEW GUINEA-BISMARCK ARCH.: Hermit Is., *ANSP 152373 (3, 34.3–47.7), *USNM 263308 (1, 24.8), *USNM 263309 (1, 20.6), *USNM 263313 (1, 20.4); Ninigo Is., *ANSP 152370 (1, 42.8), *ANSP 152372 (3, 30.6–40.8); Manus Is., *WAM P.27826-022 (1, 30.0); Madang, USNM 205682 (1, 33.2), USNM 205683 (1, 41.6); New Britain, Mowe Harbor, CSIRO B.871 (1, 28.4), Rabaul, Dawapia Rocks, USNM 201479 (2, 34.4–34.5); Trobriand Is., USNM 205680 (4, 16.8–38.0), USNM 205681 (1, 39.6); Port Moresby, DASF F03179 (2, 37.1–41.7). WESTERN AUSTRALIA: Rowley Shoals, Clerke Reef, *WAM P.27661-002 (1, 57). EASTERN AUSTRALIA: North Escape Reef, *NTM S.10468-002 (1, 42.2); Endeavour Reef, ANSP 109680 (1, 41.0), ANSP 109681 (3, 15.2–48.0), ANSP 109725 (3, 12.5–14.2), ANSP 109726 (1, 17.4); Capricorn Group, One Tree Is., USNM 201593 (1, 50.2). KAPINGAMARINGA ATOLL: CAS 28905 (1, 34.1), CAS 28906 (1, 39.7), CAS 28907 (1, 26.8), CAS 28908 (1, 37.0), CAS 28909 (3, 34.2–40.7), CAS 28910 (1, 38.0), CAS 28911 (1, 34.9), CAS 28912 (2, 13.6–18.2), CAS 28913 (2, 32.1–37.0), CAS 28914 (3, 28.7–38.8), CAS 28915 (1, 36.6), *CAS 58010 (1, 35.0), *CAS 58011 (6, 13.3–31.2), *CAS 58012 (1, 19.1). SOLOMON IS.: Guadalcanal, USNM 212032 (1, 40.5); Bougainville, Tautsina Is., USNM 201481 (2, 28.1–35.0); Florida Is., BPBM 15648 (2, 37.6–49.9). NEW CALEDONIA: BPBM 11463 (1, 42.5), CAS 15799 (1, 37.8), CAS 15800 (1, 44.4), *MNHN 1980-488 (1, 45.0), *MNHN 1980-497 (1, 51.4), *MNHN 1980-643 (3, 18.1–26.8). SANTA CRUZ IS.: Vanikoro Is., USNM 201561 (3, 24.4–27.5). NEW HEBRIDES IS.: Vate, *USNM 276513 (1, 28.8); Espiritu Santo Is., USNM 201594 (1, 20.0). ROTUMA: *USNM 278955 (4, 28.4–41.7), *USNM 278956 (6, 21.0–39.8), *USNM 278959 (1, 19.6), *USNM 278992 (1, 41.4). SAMOA IS.: Apia, CAS-SU 8996 (1, 43.2); Pago Pago, USNM 52242 (1, 34.5); "Museum Godeffroy," BMNH 1876.5.1.37 (56.7, holotype of *Petroscirtes atrodorsalis* Günther); Longley collection presumably from Pago Pago[1], USNM 195707 (7, 39.7–58.4). GILBERT IS.: Apaiang Atoll, AMS uncat. DFH 73-36 (3, 26.6–49.5), AMS uncat. DFH 73-37 (2, 18.3–25.1); Onotoa Atoll, USNM 167327 (1, 40.0).

(Morph 4) SOROL ATOLL: ANSP 126029 (1, 51.1). IFALIK ATOLL: ANSP 124872 (1, 59.1), CAS 24698 (2, 41.5–48.6), CAS 28902 (3, 39.7–59.8), CAS 28903 (1, 47.1), CAS 28904 (2, 40.9–51.8). TRUK: BPBM 7448 (2, 24.6–39.6), *BPBM 9070 (3, 29.7–31.5), UG 4628 (2, 46.2–51.0). PONAPE: CAS 28916 (2, 37.3–39.9), CAS 28917 (1, 48.2), *USNM 223223 (18, 14.8–49.2). KOSRAE: Lelu Is., *BPBM 28225 (3, 16.0–39.8).

(Morph 5) MARSHALL IS.: Eniwetok Atoll, BPBM 6258 (1, 44.7), *BPBM 8857 (1, 38.1), *BPBM 10205 (1, 49.7); Taka Atoll, USNM 201490 (6, 22.6–43.6), USNM 201492 (2, 27.1–43.8); Rongelap Atoll, USNM 142222 (1, 35.6), USNM 142223 (1, 65.5), USNM 142224 (3, 46.0–54.0).

Meiacanthus ovalauensis Günther, Fig. 24e

Petroscirtes oualanensis Günther 1880: 35 (orig. descr.: Ovalau, Fiji Islands; lectotype BMNH 1879.5.14.582).

Petroscirtes auratus Seale 1936: 85 (orig. descr.: Suva, Fiji Islands; holotype CAS 5527).

I (1976) considered the specific name of *Petroscirtes oualanensis*, obviously in reference to the type locality "ovalau," to have been an inadvertent error and adopted the emended spelling *ovalauensis* which is used herein. I recognized the form as a subspecies of *Meiacanthus atrodorsalis*, and presented a hypothetical scenario to account for the all-yellow color pattern. Recent collections have shown *M. ovalauensis* to be widely distributed throughout the Fiji Islands. *Meiacanthus atrodorsalis* and *M. tongaensis*, its two closest relatives, are absent from the Fiji Islands. Although some populations of *M. atrodorsalis* resemble *M. ovalauensis* in having an unstriped dorsal fin, those occupying adjacent island groups (New Hebrides, Rotuma, and Samoa) differ conspicuously in having a dark stripe that extends the entire length of the fin. As discussed in the general account of the *Meiacanthus atrodorsalis* complex, *M. ovalauensis* is here recognized as a distinct species.

---

[1] In an appendix, Springer (1971) established that W. H. Longley's 1926–27 collection of "Dutch East Indies" fishes without locality data deposited at the Smithsonian Institution could have come from only three possible localities: Amboina, Banda Island, or Pago Pago, Samoa. One Longley specimen assigned to USNM 277601, a pale type 2 morph with 14 pectoral-fin rays in both fins, almost certainly came from a Banda Sea locality (see Tables 6–7). The typical type 3 color pattern and 15 pectoral-fin rays present in seven other Longley specimens (USNM 195707) are strong evidence that they came from Samoa.

Meiacanthus (Meiacanthus) tongaensis n. sp., Fig. 24f.

Meiacanthus atrodorsalis atrodorsalis (non Günther): Smith-Vaniz 1976: 103 (misidentification in part; Tonga specimens).

DESCRIPTIONS. (See Tables 1–4 for frequencies of certain meristic characters.) Dorsal fin IV, 27 or 28. Anal fin II, 17 or 18. Pectoral fin 14 or 15. Caudal fin: procurrent rays 4–6 + 5–7 = 10–13; segmented rays 11 or 12; total elements 21–24. Vertebrae: precaudal 12 or 13; caudal 22 or 23; total 35 or 36. Pleural ribs on vertebrae 3–12 or 13; epipleural ribs 13 or 14. Incisor teeth in specimens 39–67 mm, n = 18: lower jaw 20–27; upper jaw 18–24. Lateral line terminates posteriorly below level of 3rd to 7th segmented dorsal-fin ray; single mid-dorsal supratemporal pore (n = 18).

Sexual dimorphism absent in pelvic fins, moderate in caudal fin (Fig. 22) in 8 males, 38.9–67.2 mm and 10 females, 50.8–64.4 mm; pelvic fin: males 9.4–12.6% SL, females 8.4–12.8% SL; caudal fin: males 32.1–76.3% SL, females 35.3–48.8% SL. Outer lobes of caudal fin elongated in both sexes, interradial membranes of inner rays weakly incised.

COLOR PATTERN. In preservative head and body are uniformly pale and covered with minute chromatophores which are more concentrated on dorsum. (Two specimens have diffuse, dusky blotches on the postorbital region of the head which appear to be remnants of the dark postorbital stripe found in *Meiacanthus smithi* and some individuals of *M. atrodorsalis*.) Dark spot, approximately equal to pupil diameter, is on ventral half of pectoral-fin axil. Dorsal fin has a broad dark stripe on basal half to three-fourths of fin which tapers posteriorly and usually extends entire length of fin; dark stripe touches or extends slightly onto dorsum in most individuals; fin above stripe is immaculate or slightly dusky. Other fins are pale except inner rays of caudal fin and pectoral rays are narrowly outlined with melanophores.

Life colors, based on several Kodachrome slides, taken underwater of living Tongatapu specimens by John E. Randall, area as follows: head and body bright yellow-green, green more noticeable dorsally, especially on head; dark stripe in dorsal fin black, remainder of fin yellow-green. Other fins also yellowish, except central area of caudal fin hyaline with short inner rays slightly dusky.

SPECIES COMPARISONS. Allopatric member of the *Meiacanthus atrodorsalis* complex distinguishable only by color pattern; refer to general discussion of complex and Table 6.

ETYMOLOGY. The specific name refers to the Tonga Islands where this species appears to be endemic.

MATERIAL EXAMINED. Eighteen specimens, 38.9–67.2 mm SL, all from Tonga Islands.

Holotype. BPBM 30877, male 62.5 mm SL, Tongatapu, 21°14′S, 175°W, off Nukualofa, reef off Yellow Jetty; 1–2 m; 6 Mar 1983; J. E. Randall.

Paratypes. BPBM 30912 (4, 38.9–60.2), taken with the holotype; ANSP 158098 (2, 39.4–52.5), BPBM 30875 (4, 45.8–57.2) same data as holotype except 19–20 Feb 1983. USNM 203765 (7, 48.1–67.2) VaVa'u Group, Neiafu, 18°39′S, 174°00′30″W; 0–16 m; 28 Jun 1965; Te Vega Exped., Cr. 8, sta. 308.

Meiacanthus procne Smith-Vaniz

I (1976) questioned the Tahitian locality (eastern distribution limit for the genus

Meiacanthus) of a single specimen of *M. procne* collected in 1931 by Zane Grey. An exceptional Grey record of *Chaetodon plebeius* Cuvier from Tahiti is also believed to be the result of a labeling error (Springer 1982). In the absence of any additional specimens from Tahiti, I consider the record to be erroneous and *M. procne* to be a Tongan endemic. It has been taken in the same collection with *M. tongaensis*.

Based on Ektachrome transparencies taken by John E. Randall of one living and two freshly dead specimens from Neiafu, the life coloration of *M. procne* is as follows: venter and pelvic and anal fins white; pale areas of the remaining fins light gray to white. Ventral half of head and body white becoming pale gray to bluish-gray dorsally. Heavily pigmented areas of body and fins dark gray or black.

NEW MATERIAL. All from Neiafu, Tonga Islands: BPBM 30880 (2, 35.7–34.1), BPBM 30881 (3, 26.6–31.6), BPBM 30882 (3, 29.8–34.4).

Meiacanthus reticulatus Smith-Vaniz, Fig. 25

Previously known only from the female holotype, a recent collection from Osprey Reef listed below extends the range of *M. reticulatus* approximately 800 km to the southwest. Morphometric data obtained from the new specimens (one male, 59.2 mm SL and two females, 39.3–62.8 mm) indicate that *M. reticulatus* has nonsexually dimorphic pelvic and caudal fins: total ranges for the species 9.7–10.9% SL and 41.7–53.9% SL, respectively. Meristic data are similar or identical with that previously reported. In life, the background coloration of the body and head is light olive-buff, overlaid with numerous brown speckles. The dorsal, anal, and pelvic fins and outer rays of the caudal fin are dark sooty-brown. The iris is bright blue. Two of the new specimens and the living individual shown in Fig. 25 differ from the holotype in having a narrow, dark postorbital stripe that extends to below the anterior third of the dorsal fin.

NEW MATERIAL. Coral Sea, Osprey Reef, 13°53′S, 146°32′E, BPBM 31738 (3, 39.3–62.8).

Meiacanthus bundoon Smith-Vaniz

New locality records for *M. bundoon* are given below. Originally described from five specimens from Fiji, the range of the

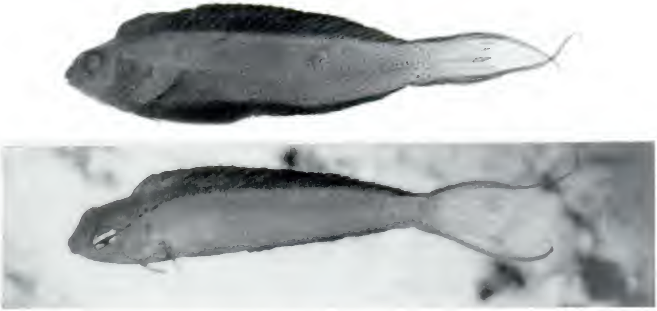


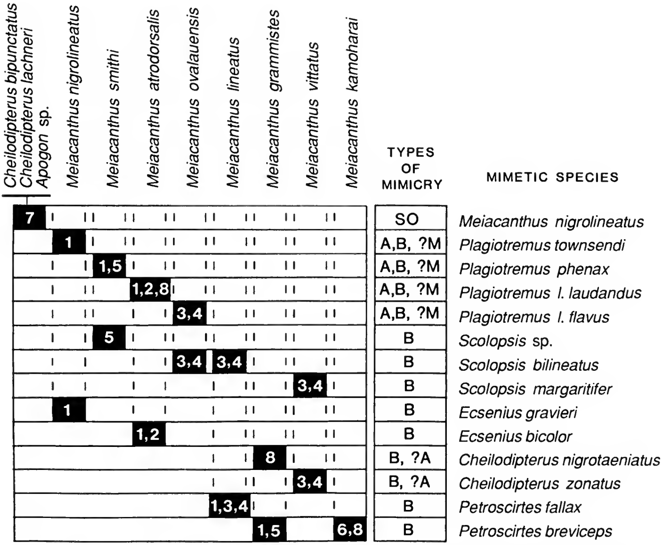
FIG. 25. *Meiacanthus reticulatus*. **Above**, Egum Atoll, Solomon Sea, female, 70.5 mm SL; **Below**, Osprey Reef, Coral Sea (based on a color slide taken by Robert M. Pyle; fish not collected).

species is extended to the Tonga Islands, where it occurs sympatrically with *M. ditrema* and *M. tongaensis*.

NEW MATERIAL. TONGA ISLANDS: Tongatapu, BPBM 30878 (6, 26.0–56.3). FIJI ISLANDS: Ono-i-lau, 21°38′S, 178°45′W, USNM 236028 (1, 33.8); Lau Is., Navutu Ira I., 18°55′S, 178°33′W, USNM 236029 (1, 51.2); Totoya I., 18°58′57″S, 179°52′12″W, USNM 236030 (1, 39.3).

MIMETIC ASSOCIATIONS INVOLVING *MEIACANTHUS* SPECIES

Although mimicry is relatively uncommon in marine fishes (Russell et al. 1976), at least eight species of *Meiacanthus* are known or suspected models in Batesian or Aggressive mimetic interactions, Fig. 26. This is not too surprising as all species of *Meiacanthus* have a pair of large, elaborately grooved, dentary canines at the base of which sits a well-developed gland (Fishelson 1974). Laboratory experiments have clearly shown that *Meiacanthus* can inflict a noxious bite which causes a wide variety of naive predators to reject them alive and unharmed after ingestion (Losey 1972; Springer and Smith-Vaniz 1972). Given such an effective antipredator device, it



Cheilodipterus bipunctatus *Cheilodipterus lachneri* *Apogon* sp.	*Meiacanthus nigrolineatus*	*Meiacanthus smithi*	*Meiacanthus atrodorsalis*	*Meiacanthus ovalauensis*	*Meiacanthus lineatus*	*Meiacanthus grammistes*	*Meiacanthus vittatus*	*Meiacanthus kamoharai*	TYPES OF MIMICRY	MIMETIC SPECIES
7									SO	*Meiacanthus nigrolineatus*
	1								A,B, ?M	*Plagiotremus townsendi*
		1,5							A,B, ?M	*Plagiotremus phenax*
			1,2,8						A,B, ?M	*Plagiotremus l. laudandus*
				3,4					A,B, ?M	*Plagiotremus l. flavus*
		5							B	*Scolopsis* sp.
				3,4	3,4				B	*Scolopsis bilineatus*
							3,4		B	*Scolopsis margaritifer*
	1								B	*Ecsenius gravieri*
			1,2						B	*Ecsenius bicolor*
						8			B, ?A	*Cheilodipterus nigrotaeniatus*
							3,4		B, ?A	*Cheilodipterus zonatus*
					1,3,4				B	*Petroscirtes fallax*
						1,5		6,8	B	*Petroscirtes breviceps*

FIG. 26. Documented or suspected mimetic associations involving species of *Meiacanthus*. Presumed models are at top of figure. Abbreviations for types of mimicry: SO, school oriented; A, aggressive; B, Batesian; M, Müllerian. Numbers (1–8) refer to primary literature sources documenting mimetic associations: 1, Springer and Smith-Vaniz (1972); 2, Losey (1972); 3, Allen et al. (1975); 4, Russell et al. (1976); 5, Smith-Vaniz (1976); 6, Yatsu et al. (1983); 7, Dafni and Diamant (1984); and 8, present paper.

may seem incongruous that a species of *Meiacanthus* might itself mimic another species. As discussed under the account of *M. nigrolineatus*, just such an interaction apparently occurs between juveniles of that species and juveniles of several species of cardinal fish.

When one species mingles with a school of another species of similar appearance and thus gains an advantage by appearing inconspicuous to potential prey (e.g. the familiar wolf in sheep's clothing scenario), this is clearly a case of what has been appropriately termed "Aggressive mimicry." In my general discussion of mimicry, I (1976) questioned what to call interactions between schooling species where the benefit gained from the association was inconspicuousness to potential predators. Although several examples of this type of mimicry have been described, until recently no precise term had been coined for it. According to Dafni and Diamant (1984), "School-oriented mimicry" applies to situations where a solitary or nongregarious species gains a protective advantage by blending into aggregations of superficially similar species. A classical example of this type of mimicry (Starck 1969) is the affinity of *Ecsenius midas* Starck for schools of *Anthias squamipinnis* (Peters).

The extent to which Müllerian mimicry plays a role, if at all, in *Plagiotremus-Meiacanthus* mimetic interactions is unclear. Springer and Smith-Vaniz (1972) established that at least one potential *Meiacanthus* predator, *Pterois volitans* Linnaeus, also rejects *Plagiotremus townsendi* as prey (Müllerian mimicry). The cause of this unacceptability is unknown but is believed to be taste. In subsequent laboratory experiments Springer (pers. comm.) found that *Pterois* rejected both live and dead *P. townsendi*. Considering the close phylogenetic relationship of the two other species of *Plagiotremus* that comprise the subgenus *Musgravius* Whitley, it is likely that in some situations *P. phenax* and *P. laudandus* may also function as Müllerian mimics.

It seems probable that the two species of *Cheilodipterus* that are known or suspected Batesian mimics of a *Meiacanthus* may also be Aggressive mimics. *Cheilodipterus* species are predators of small fishes and crustaceans, and typically tend to hide in caves and deep crevices during the day. Because species of *Meiacanthus* feed almost exclusively on small benthic invertebrates or zooplankton, small fishes should have no fear of them. A *Cheilodipterus* that is diurnally active and mimics a *Meiacanthus* would likely benefit from greater ease in approaching small fish prey.

Genus **Plagiotremus** Gill

Except for the synonymization of *P. celebesensis* (Herre), the composition of *Plagiotremus* remains unchanged. Most new observations regarding species of *Plagiotremus* involve distributional records. The following key is given as an identification aid.

1a. Preanal length 22.8–28.2 percent SL; total dorsal-fin elements 66–73; segmented anal-fin rays 54–60 (western Pacific).... *P. spilistius* Gill
1b. Preanal length 34.0–52.8 percent SL; total dorsal-fin elements 32–54; segmented anal-fin rays 19–40.............................. 2
2a. Pelvic fins absent, at least in adults; segmented anal-fin rays 40; total dorsal-fin elements 53–54; dentary incisors with tips arrowhead-shaped, Fig. 27a (Sulu Archipelago) .... *P. iosodon* Smith-Vaniz
2b. Pelvic fins present; segmented anal-fin rays 19–33; total dorsal-fin elements 32–48; dentary incisors with tips chisel-shaped, ovoid or bluntly lanceolate, Figs. 27b–d...............3
3a. Body of adults without stripes; snout of adults not fleshy, blunt; segmented anal-fin rays 19–24 4
3b. Body of adults striped; snout of adults fleshy, conical; segmented anal-fin rays 27–33........6
4a. Longest caudal-fin ray 25.5–51.6 percent SL; dorsal-fin spines 7–10, usually 9 (western and central Pacific)..........*P. laudandus* (Whitley)
4b. Longest caudal-fin ray 18.0–25.5 percent SL; dorsal-fin spines 6–8........................5
5a. Dorsal fin with dark stripe entire length of fin; total dorsal-fin elements 35–37 (eastern Indian Ocean)................*P. phenax* Smith-Vaniz

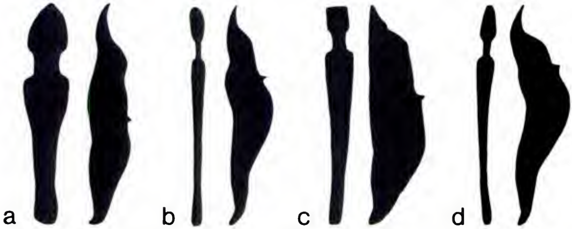


FIG. 27. Anterior and lateral views of dentary incisors in selected species of *Plagiotremus*. **a**, *P. spilistius;* **b**, *P. laudandus;* **c**, *P. rhinorhynchos;* **d**, *P. tapeinosoma*. (From Smith-Vaniz 1976, fig. 72)

5b. Pigmentation of dorsal fin not as above; total dorsal-fin elements 32–34 (Red Sea and Gulf of Oman). . . . . *P. townsendi* (Regan)

6a. Innermost caudal-fin ray of adults pigmented like adjacent rays; dentary incisors with tips chisel-shaped, Fig. 27c; dorsal-fin spines 10–12 (usually 11); two pairs of interorbital pores. 7

6b. Innermost caudal-fin ray of adults distinctly darker than adjacent rays, at least proximally; dentary incisors with tips ovoid or bluntly lanceolate, Fig. 27d; dorsal-fin spines 7–9 (usually 8); single pair of interorbital pores. 8

7a. Background coloration of adults usually brown or brownish-black (Indo-west Pacific, excluding Hawaii). . . . . *P. rhinorhynchos* (Bleeker)

7b. Background coloration of adults yellow-orange (Hawaiian Islands). . . . . *P. ewaensis* (Brock)

8a. Anal fin immaculate; posterior two-thirds of dorsal fin with intense dark stripe; caudal fin of adults frequently exceeds 20 percent SL (eastern Pacific Ocean). . . . . . *P. azaleus* (Jordan)

8b. Anal fin dusky, at least distally; pigmentation of dorsal fin not as above; caudal fin of adults rarely exceeds 20 percent SL. 9

9a. Dark mid-lateral stripe very irregular, largely broken into disconnected series of vertically elongate blotches (Indo-west Pacific, excluding Hawaii). . . . .*P. tapeinosoma* (Bleeker)

9b. Dark mid-lateral stripe of nearly uniform intensity, if present spots are always connected by stripe (Hawaiian Islands). .*P. goslinei* (Strasburg)

Plagiotremus spilistius Gill

I (1976) provisionally recognized *Plagiotremus celebesensis* (Herre) as a valid species, but noted that the two known specimens, both from Lembeh Strait, are juveniles (54.5–54.9 mm SL) and that the presence of minute pelvic fins is the only reliable character that distinguishes them from *P. spilistius* (known only from adults 120–174 mm SL), which lacks pelvic fins. The intermediacy of the color pattern, pelvic fin length, and number of incisor teeth (Table 8) exhibited in a subsequently collected specimen from Irian Jaya establishes *P. celebesensis* as a junior synonym of *P. spilistius*. This specimen has the dark dorsal and anal fins characteristic of *P. spilistius* but lacks the dark spot on the anterodorsal margin of the pectoral fin present in larger specimens.

Based on all available specimens of *P. spilistius*, the ranges for certain meristic characters are as follows: dorsal fin rays X, 56–63; anal fin rays II, 54–60; vertebrae 15–16 + 54–62 = 69–78 total; dorsal and ventral procurrent caudal-fin rays 5 or 6, respectively; total procurrent caudal-fin

TABLE 8. Ontogenetic changes in dentition and pelvic fin length (percent SL) in *Plagiotremus spilistius*

Standard length mm (Number of individuals)	54.5–54.9 (2)	89.5 (1)	130–164 (4)
Pelvic fin length	1.5–1.6	0.6	absent
Premaxillary incisors	21–22	32	42–44
Dentary incisors	20–23	40	46–49

rays 10–12; total caudal-fin elements 21–23. The combination of dentary incisors with arrowhead-shaped tips, absence of pelvic fins in adults, and relatively high numbers of vertebrae and segmented dorsal- and anal-fin rays will distinguish *P. spilistius* and *P. isodon* Smith-Vaniz, which are the sole members of the subgenus *Plagiotremus*, from their eight congeners. They also differ from their congeners in their apparent rarity, perhaps a reflection of different habitat or behavioral preferences; all specimens for which capture data are available have either been trawled, attracted to a night-light, or were taken in a dynamite collection. The known distributions of *Plagiotremus spilistius* and *P. isodon* are shown in figure 28.

NEW MATERIAL. IRIAN JAYA: S coast off Paulau Adi Is., 4°5.3′S, 133°31.3′E; trawled in 46–51 m; 5 Jul 1979; sta. BBC-1742; USNM 222106 (1, 89.5). PHILIPPINES: Samar Sea, Carigara Bay, 11°30′N,

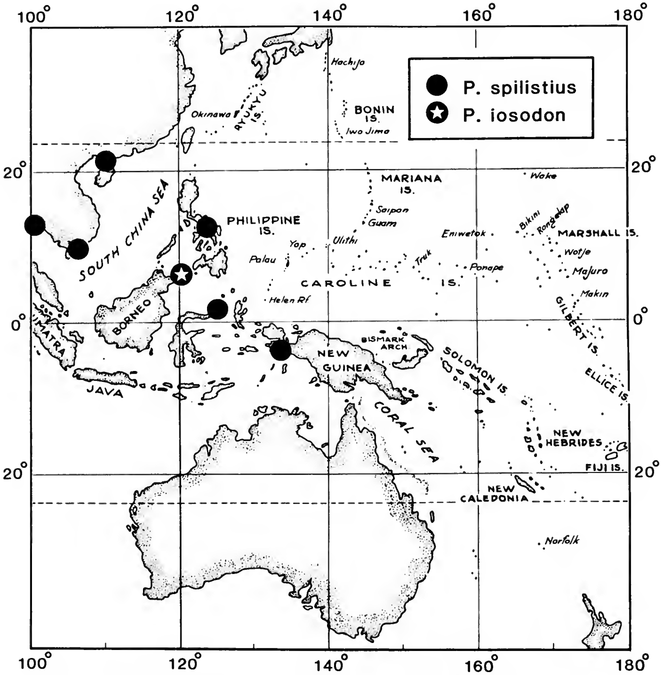


FIG. 28. Distribution of the two *Plagiotremus* species comprising the subgenus *Plagiotremus*.

124°40′30″E; trawled in 65–70 m; 7 Feb 1980; USNM 224476 (1, 130.0).

Plagiotremus laudandus (Whitley)

The known geographic distribution of *P. laudandus* (Fig. 29) is expanded on the basis of 51 additional specimens, including several new records, cited below. The occurrence of the species at American Samoa, its easternmost distributional limit, is based on a Kodachrome transparency taken underwater by John E. Randall of a living specimen from Tutuila Island. This new material does not alter the range of meristic values previously reported for the species, but does allow a more critical assessment of geographic variation with respect to color pattern.

All members of the subgenus *Musgravius*, including *Plagiotremus laudandus* (both subspecies), *P. townsendi* and *P. phenax*, are aggressive (and perhaps Müllerian) mimics of a sympatric species of *Meiacanthus*, and each of these *Plagiotremus-Meiacanthus* pairs is allopatric. I (1976) hypothesized that the occurrence of this type of specialized interaction exclusively (other *Plagiotremus* species clearly are not *Meiacanthus* mimics) and consistently in a subgroup of congeners had a genetic basis, and used it as one of several synapomorphies supporting monophyly of the group. I noted that in specimens of *P. laudandus laudandus* the dark submarginal stripe present in the dorsal fin is variously developed, ranging from being restricted to the spinous part of the fin to extending the entire length of the fin. The extent to which such variation occurred was not discussed. Now that the geographic distributions and range of variation in color patterns in members of the *Meiacanthus atrodorsalis* complex are better known, it is apparent (with one exception discussed below) that the color pattern of *P. laudandus* closely parallels that of its sympatric *Meiacanthus* model.

When I (1976) described *Plagiotremus laudandus flavus*, it was known only from Fiji where it replaces the allopatric, nominal subspecies and has an essentially all yellow color pattern similar to that of the Fijian endemic *Meiacanthus ovalauensis*. I stated that if the coloration of *flavus* is an

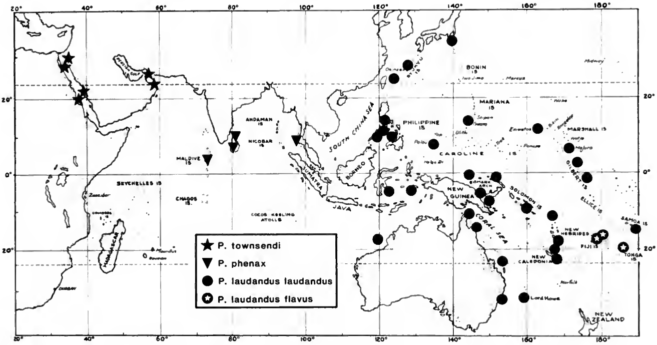


FIG. 29. Distribution of the three *Plagiotremus* species comprising the subgenus *Musgravius*.

ecophenotypic manifestation, subspecific recognition is unjustified. The recent collection of *P. laudandus flavus* from the Tonga Islands where it occurs sympatrically with *Meiacanthus tongaensis*, from which it is easily distinguished by the lack of a conspicuous black stripe along the base of its dorsal fin, strongly suggests that color pattern in *flavus* is genetically controlled. Based on a Kodachrome slide provided by John E. Randall, the life coloration of the Tongan *Plagiotremus* is virtually identical to Fijian specimens. The only exception is one of four females collected that has a narrow black stripe along the distal margin of the spinous dorsal fin. The exceptional nature of the lack of precise agreement in the color pattern of this Tongan *Plagiotremus-Meiacanthus* pair suggests that the *Plagiotremus* became established there relatively recently, and that there has not been enough time for selection pressures to produce a better *Plagiotremus* color mimic.

NEW MATERIAL. (*Plagiotremus laudandus laudandus*) PHILIPPINES: Batangas, Sombrero Is., USNM 228923 (1, 23.0); Palawan Province, Cocoro Is., USNM 263299 (1, 32.4), Puerto Princesa Bay, USNM 263319 (1, 26.0); Balicasag Is., USNM 263321 (1, 37.0). BANDA SEA: Ceram, Marsegoe Bay, AMS I.18469-087 (1, 34.4). NEW GUINEA-BISMARCK ARCH.: Hermit Is., ANSP 152375 (1, 39.6), USNM 263315 (3, 30.8–35.1); Ninigo Is., ANSP 152374 (1, 33.5), USNM 263318 (1, 38.6); New Ireland vicinity, USNM 263320 (2, 23.1–40.8); Massas Is., USNM 263316 (4, 22.8–32.8). WESTERN AUSTRALIA: Rowley Shoals, Mermaid Reef, NTM S.11230-001 (4, 39.4–41.8). EASTERN AUSTRALIA: Raine Is., 11°35′S, 144°2′20″E, AMS I.20756-043 (1, 32); Lizard Is., AMS I.19441-014 (1, 45); Yonge Reef, AMS I.19445-046 (1, 40); Escape Reef, AMS I.22584-002 (1, 30); Seal Rocks, 32°28′S, 152°33′E, AMS I.18292-002 (1, 26.6). NEW CALEDONIA: Noumea, USNM 263317 (1, 39.7).

(*Plagiotremus laudandus flavus*) FIJI ISLANDS: Viti Levu, 18°8′51′S, 178°24′9″E, USNM 236047 (2, 24.4–39.3); Navutu Ira Is., 18°55′S, 178°33′W, USNM 236046 (2, 37.5–38.2); Ono-i-lau, 20°37′S, 178°40′W, USNM 236045 (17, 37.2–53.7). TONGA ISLANDS: Tongatapu, 21°14′S, 175°W, BPBM 30883 (1, 54.9), BPBM 30884 (3, 41.4–56.0).

Plagiotremus phenax Smith-Vaniz

Previously known only from Sri Lanka and the Maldive Islands, the range of the species is extended eastward to the Similan Islands (8°34′N, 97°38′E) northwest of Phuket, Thailand, on the basis of a Kodachrome slide taken underwater by John E. Randall of a living specimen. The more extensive geographical distribution of *P. phenax* is expected as it is a close mimic of *Meiacanthus smithi*, which has a nearly identical distribution pattern.

Plagiotremus townsendi (Regan)

Previously known only from the Gulf of Aqaba and single specimens from off Port Sudan and the Merkran coast of Iran, the specimens listed below represent new records for the species. These additional specimens agree in all major details, including life coloration, with Gulf of Aqaba specimens.

NEW MATERIAL. RED SEA: Jeddah Harbor, USNM 217347 (1, 26.4), USNM 217349 (6, 28.9–41.1), USNM 217359 (1, 34.2); Khor Obhour, 35 km N of Jeddah, ANSP 152019 (1, 37.2). GULF OF OMAN: Sidab, Muscat, just N of Bander Sidab Bay, USNM 217333 (3, 20.4–33.8).

ACKNOWLEDGMENTS

I am grateful to the following individuals for the loan of specimens or accommodations and other courtesies during visits to their institutions: Douglass F. Hoese and John R. Paxton (AMS); Alwyne Wheeler (BMNH); John E. Randall and Arnold Y. Suzumoto (BPBM); M. Eric Anderson, David Catania, and William N. Eschmeyer (CAS); Marie Louise Bauchot and Martine Desoutter (MNHN); Helen K. Larson and Barry C. Russell (NTM); Jeffery W. Johnson and Roland J. McKay (QMB); Phillip C. Heemstra (RUSI); Victor G. Springer (USNM); and Gerald R. Allen (WAM). Patricia J.Kailola provided important collection data. Thanks are also due

Douglass F. Hoese, Hitoshi Ida, Rudie H. Kuiter, Edward O. Murdy, Robert M. Pyle, Barry C. Russell, Jeffery T. Williams, and, especially, John E. Randall for providing specimen photographs and underwater color slides. Eugenia B. Böhlke made most of the radiographs utilized in this study, and Dorothy Viola typed the manuscript.

Partial travel support was provided by the Smithsonian Institution's Leonard P. Schultz Fund which facilitated travel within Australia and allowed me the opportunity to discover important unidentified collections that would not otherwise have been available. Finally, I wish to acknowledge the continued advice and friendship of Victor G. Springer, whose encouragement prompted this update.

LITERATURE CITED

ADAMS, A. 1850. Preface. Pages v–viii *in* The zoology of the voyage of H.M.S. "Samarang"; under the command of Captain Sir Edward Belcher, during the years 1843–1846. London.

ALLEN, G. R., B. C. RUSSELL, B. A. CARLSON, AND W. A. STARCK, II. 1975. Mimicry in marine fishes. Tropical Fish Hobbyist 24(1): 47, 49, 52–56.

AMESBURY, S. S. AND R. F. MYERS. 1982. The Fishes. Pages 1–141 *in* Guide to the coastal resources of Guam, 1.

ARAI, R. AND H. IDA. 1975. The sea fishes of Yakushima and Tanegashima Islands, southern Kyushu, Japan. Memoirs of the National Science Museum 8: 183–198. (In Japanese)

BURGESS, W. E. AND H. R. AXELROD. 1972. Pacific marine fishes 1: 1–280, 489 figs. T. F. H. Publications, Inc., Neptune City.

——— and ———. 1972. Pacific marine fishes 2: 283–560, 552 figs.

——— and ———. 1975. Pacific marine fishes 6: 1387–1654, 479 figs.

——— and ———. 1976. Pacific marine fishes 7: 1658–1925, 412 figs.

DAFNI, J. AND A. DIAMANT. 1984. School-oriented mimicry, a new type of mimicry in fishes. Marine Ecology—Progress Series 20: 45–50.

FERRARIS, C. J., JR. AND E. O. MURDY. 1981. Aspects of sexual dimorphism and feeding in *Petroscirtes variabilis* Cantor (Osteichthys: Blenniidae). Micronesia 17(1–2): 157–159.

FISHELSON, L. 1974. Histology and ultrastructure of the recently found buccal toxic gland in the fish *Meiacanthus nigrolineatus* (Blenniidae). Copeia 1974(2): 386–392.

FOWLER, H. W. 1946. A collection of fishes obtained in the Riu Kiu Islands by Captain Ernest R. Tinkham A.U.S. Proceedings of The Academy of Natural Sciences of Philadelphia 98: 123–218.

GÜNTHER, A. C. L. G. 1877. Andrew Garrett's Fische der Sudsee. IV. Journal des Museum Godeffroy 13: 169–216.

———. 1880. Report on the shore fishes procured during the voyage of H.M.S. Challenger in the years 1873–1876. Zoology 1(6): 1–82.

KORENKE, L. W. 1984. Cenozoic tectonic development of the Southwest Pacific. United Nations Economic and Social Commission for Asia and the Pacific Committee for Coordination of Joint South Pacific Offshore Areas, Technical Bulletin 6, 126 pp.

LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in Herpetology and Ichthyology. Copeia 1985(3): 802–832.

LOSEY, G. S. 1972. Predation protection in the poison-fang blenny, *Meiacanthus atrodorsalis*, and its mimics *Ecsenius bicolor* and *Runula laudandus* (Blenniidae). Pacific Science 26(2): 129–139.

MASUDA, H., K. AMAOKA, C. ARAGA, T. UYENO, AND T. YOSHINO. 1984. The Fishes of the Japanese Archipelago. Tokai University Press. 437 pp., 370 pl.

MILSOM, J. AND M. G. AUDLEY-CHARLES. 1986. Post-collision isostatic readjustment in the southern Banda Arc. Pages 353–364 *in* M. P. Coward and A. C. Ries, eds. Collision tectonics. Geological Society Special Publication, 19.

PENRITH, M. J. 1976. Distribution of shallow water marine fishes around southern Africa. Cimbebasia, ser. A, 4(7): 137–154.

RANDALL, J. E. AND H. A. RANDALL. 1960. Examples of mimicry and protective resemblance in tropical marine fishes. Bulletin of Marine Science of the Gulf and Caribbean 10(4): 444–480.

ROBINSON, G. S. 1975. Macrolepidoptera of Fiji and Rotuma: a taxonomic and biogeographic study. E. W. Classey Ltd., Faringdon. 362 pp.

RUSSELL, B. C., G. R. ALLEN, AND H. R. LUBBOCK. 1976. New cases of mimicry in marine fishes. Journal of Zoology, London 180: 407–423.

SEALE, A. 1936. A new member of the blenny family. Proceedings of the California Academy of Sciences 23(6): 85–86.

SMITH-VANIZ, W. F. 1976. The saber-toothed blennies, tribe Nemophini (Pisces: Blenniidae). The Academy of Natural Sciences of Philadelphia, Monograph 19, 196 pp.

SPRINGER, V. G. 1971. Revision of the fish genus *Ecsenius* (Blenniidae, Blenniinae, Salariini). Smithsonian Contributions to Zoology 72: 1–74.

———. 1982. Pacific plate biogeography, with special reference to shorefishes. Smithsonian Contributions to Zoology 367: 1–182.

——— AND W. F. SMITH-VANIZ. 1972. Mimetic relationships involving fishes of the family Blenniidae. Smithsonian Contributions to Zoology 112: 1–36.

STARCK, W. A. 1969. *Ecsenius* (*Anthiiblennius*) *midas*, a new subgenus and species of mimic blenny from the western Indian Ocean. Notulae Naturae of The Academy of Natural Sciences of Philadelphia 419, 9 pp.

WHITLEY, G. P. 1961. Fishes from New Caledonia. Proceedings of the Royal Zoological Society of New South Wales 1958–1959: 60–65.

WICKLER, W. 1968. Mimicry in plants and animals. McGraw-Hill Book Company, New York. 255 pp.

YATSU, A., A. IWATA, AND M. SATO. 1983. First records of the blenniid fishes, *Petroscirtes springeri* and *Petroscirtes variabilis*, from Japan. Japanese Journal of Ichthyology 30(3): 297–300.

PUBLICATION NOTICE

The preceding paper is a supplement to: **The Saber-Toothed Blennies, Tribe Nemophini (Pisces: Blenniidae),** by William F. Smith-Vaniz. Monograph 19 of The Academy of Natural Sciences of Philadelphia. 1976. 196 pp. $17, U.S. and Canada; $19, other.

Available from: Scientific Publications, The Academy of Natural Sciences of Philadelphia, 19th and the Parkway, Philadelphia, PA 19103.

Proceedings of The Academy of Natural Sciences of Philadelphia 139: 53–64, 1987.

Ryckholt's *Mélanges Paléontologiques*, 1851–1862, with a New Name for *Tudicula* H. & A. Adams, non Ryckholt

GARY ROSENBERG
Department of Mollusks, Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138

RICHARD E. PETIT
Research Associate, Department of Invertebrate Zoology, Smithsonian Institution, Washington, DC 20560

ABSTRACT.—Ryckholt's little known and seldom cited *Mélanges Paléontologiques* is discussed and dated. His names for invertebrate taxa of generic rank, most of which are mollusks from the Devonian, Carboniferous, and Cretaceous of Belgium, are discussed and shown to be available. The genus *Tudivasum* nom. nov. (Gastropoda: Turbinellidae: Vasinae) is proposed to replace *Tudicula* H. & A. Adams 1864, which is preoccupied by *Tudicula* Ryckholt 1862. The resulting new combinations are listed. This replacement eliminates the confusion of *Tudicula* H. & A. Adams with *Tudicla* Röding 1798, which is also in the Turbinellidae. [Belgium, Carboniferous, Cretaceous, Devonian, Mollusca, Ryckholt, *Tudicla*, *Tudicula*, *Tudivasum*, Turbinellidae]

Between 1851 and 1862, Baron Philippe de Ryckholt published *Mélanges Paléontologiques*, a three-part work on Belgian invertebrate fossils. The *Mélanges*, in its entirety, is very rare and seldom cited. We know of only five complete copies of the *Mélanges:* at Yale University (New Haven, Connecticut); the United States Geological Survey Library (Reston, Virginia); the Institut Royal des Sciences Naturelles de Belgique (Brussels); the British Museum (Natural History); and in the private library of the junior author. The British Museum did not complete its set until 1956 (J. Cooper pers. comm.).

We have little information about Ryckholt. He was a "lieutenant-colonel d'artillerie" and a "chevalier de l'ordre de Léopold" according to Crosse (1863:216). Ryckman de Betz (1957: 90–91) lists him as Philippe-Louis-François-Joseph-Adrien of the de Bounam de Ryckholt family and states that the titles Chevalier and Baron were hereditary. Dewalque (1874: 157) states that Ryckholt died in 1874 and discusses the fate of his collections. In addition to the *Mélanges*, Ryckholt published seven other scientific works. These include an article on fossil chitons (1845), one on fossil cephalopods (1852), and five articles on various subjects in *Journal de Conchyliologie* (1860a–b, 1862a–c). *Mélanges Paléontologiques* is Ryckholt's most important and extensive work.

The *Mélanges* contains descriptions and illustrations of several hundred new taxa, the names of which have been overlooked by most nomenclators. The purpose of this report is to determine the dates of publication of the *Mélanges*, to establish the availability of the names that Ryckholt introduced, particularly in the third part, and to make any necessary nomenclatural changes resulting from their availability.

DATES OF PUBLICATION

The first part of the *Mélanges*, consisting of 176 pages and 10 plates, appeared in volume 24 of *Mémoires Couronnés et*

Mémoires des Savants Étrangers for 1850–1851, published by the Académie Royale de Belgique in 1852. However, as Woodward (1913: 1775) and Neave (1940, 3: 270) note, Ryckholt distributed separates in 1851. *The Quarterly Journal of the Geological Society of London* [1852, 8(1): 96] records that he donated a copy of Part 1 to the Society's library between 1 July and 31 October 1851. Part 1 was not published before 1851 as Ryckholt mentions this date in footnotes within the work (pp. 38, 54).

In the text of the first part, Ryckholt uses the dates 1847 and 1850 when referring to his new species. Some subsequent authors have taken these as dates of publication for the names. However, 1847 is the year when Ryckholt first presented the manuscript of Part 1 of the *Mélanges* to the Académie (Ryckholt 1851: 60), under the title "Élucubrations paléontologiques, 1^re^ partie" [*Bulletin de l'Académie Royale*, 1847, 14(10): 238]. Dumont and Cantraine (1848) reviewed the manuscript and recommended it for publication. Despite this recommendation, it was not then published. Ryckholt (1854: 72) states that his work was interrupted by "*les événements politiques, qui marquèrent le commencement de l'année 1848* . . . ," presumably referring to the overthrow of the French government in February 1848 and the resulting Belgian neutrality crisis (Ridder 1928). In 1850 Ryckholt added descriptions of thirty species to the manuscript and made nomenclatural changes, then resubmitted it under the title *Mélanges Paléontologiques*. Dumont reviewed the revised manuscript in November, 1850 and recommended it for publication. The years 1847 and 1850 that Ryckholt uses for his new names, and the date at the end of the *Introduction* (p. 8), "Gand, le 20 septembre, 1847," thus represent times of completion of parts of the manuscript, rather than dates of publication. Similar, misleading internal dates occur in many works of the era. The true date of publication for the first part of the *Mélanges* and the nominal taxa introduced therein is not later than 30 October 1851.

The second part of the *Mélanges*, consisting of 205 pages and plates 11 to 20, has the date "Gand, décembre 1853" at the end of the *Introduction* (p. 22). Woodward (1913: 1775) records this date, but includes the notation, "Brussels? 1854?" The correspondence section in *Bulletin de l'Académie Royale* shows that Ryckholt presented the manuscript of Part 2 to the Académie on 1 April 1854 [21(4): 209], then withdrew it in August [21(10): 138]. Dewalque (1879: 159) repeats these dates and states that Ryckholt published at his own expense. Thus, Part 2 was privately printed not earlier than August 1854; December 1853 is when the *Introduction* was written.

The third part of the *Mélanges* consists only of 16 plates, numbers 21 to 36, with captions thereon, published singly between January 1860 and June 1862, along with the title and errata pages for that part. The errata page says "*Observation:* Ces planches ont été distribuées, à la date renseignée à l'entête de chacune d'elles, aux paléontologues les plus particulièrement intéressés à les connaître." Briart and Cornet (1870: 19; 1871: 2) state that a text was never issued; we have no evidence that one was ever written.

The distribution of these plates is confirmed by a review (Crosse 1863), by mention in *Bulletin de la Société Malacologique de Belgique* for 1865 (1: lxxxiv), by the citations of Ryckholt (1862c: 414–417) and Briart and Cornet (1870: 19, 27, 33, 37; 1871: 2, 4), and by the bibliography in Mourlon (1881: 368). The *Bulletin* and Mourlon cite all 36 plates in the complete work, as does Hermann (1900: 28), who advertised a complete set of the *Mélanges* for 30 francs. In addition, in a list of Cretaceous fossils of Belgium, Dewalque (1868; 1880: 439–443) records many of the taxa named in the third part, including the genera *Astreidomus, Guildfortia, Lithariodomus, Phyllicocheilus, Rhealaria,* and *Torculina,* and incorporates changes from the errata page. Mourlon (1881: 84–88) reprinted Dewalque's list. Furthermore, Ubaghs (1879: 129, 203) lists *Vermetus pselionopsis* Ryckholt, which was figured on plate 23 (1860) and Fritsch (1910: 16, pl.6, fig. 2) named the genus *Ryckholtia* (Gastropoda) based on species figured on Ryckholt's plate 26. Although distributed in irregular fashion, Part 3 of the *Mélanges* was referred to in at least eight works by seven authors in the twenty years following its appearance. All three parts of the *Mélanges* therefore must be considered published in the sense of the International Code of Zoological Nomenclature (ICZN), and the new names therein must be considered available.

Our collation of the complete work therefore is:

RYCKHOLT, BARON PHILIPPE DE. 1851–1862. *Mélanges Paléontologiques.*

1851. Part 1. Mémoires Couronnés et Mémoires des Savants Étrangers de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique, 24: 1–176, plates 1–10.

1854. Part 2. [Privately printed.] Pages 1–205, plates 11–20.

1860–62. Part 3. [Privately printed.] Plates 21–36. [No text, but with title page and unnumbered errata page. Most plates are individually dated:] 21, Janvier 1860; 22, Mars 1860; 23, undated; 24, Juin 1860; 25, Septembre 1860; 26, Novembre 1860; 27, Janvier 1861; 28, Janvier 1861; 29, Mars 1861; 30, Avril 1861; 31, Septembre 1861; 32, undated; 33, Mars 1862; 34, Mars 1862; 35, Juin 1862; 36, Juin 1862.

RYCKHOLT'S NOMINAL TAXA

Ryckholt named more than 550 taxa in the *Mélanges:* 136 species and 5 genera in Part 1, 120 species and 5 genera in Part 2, and 297 species and 9 genera in Part 3. This tally includes replacement names but not nomina nuda or otherwise unavailable names. Most of these names are for mollusks, but a few are for annelids, brachiopods, coelenterates, or echinoderms.

The molluscan names introduced by Ryckholt in the third part of the *Mélanges* have been overlooked by most nomenclators except Ruhoff (1980), who had access to the copy in the library of the junior author. Ruhoff's dating of the names of Ryckholt's species is in some cases incorrect; the collation above will allow determination of the proper dates. Taxonomists should note that Ryckholt sometimes changed the generic placements and trivial names of his taxa in footnotes. Ruhoff missed some of these changes.

In the opinion of Dr. Dhondt (pers. comm.) the species figured in Part 3 are nomina dubia, and "[the] drawings were made with a lot of imagination from poor specimens or even worse from moulds." Criticism of Ryckholt's figures is not restricted to those in the third part: Knight (1941: 204) called Ryckholt's figure of *Naticodon globosum* (pl. 3, fig. 12) "a fanciful restoration." Remnants of Ryckholt's collections are housed in the Institut Royal des Sciences Naturelle de Belgique, but Dr. Dhondt advises that ". . . what he describes is not only absent in his collections but is often not to be found even in the locality he indicates as the type locality." Dewalque (1879: 158) states that some of Ryckholt's material went to the university in Liége, but Cleevely (1983: 252, 343) and Dhondt do not indicate that any remains there.

Although many of Ryckholt's taxa in Part 3 are probably unrecognizable, and seem not to have been cited in the 20th century by anyone other than Ruhoff (1980), their names are available as they were validly introduced into the literature. Several workers before 1900 did treat taxa from the third part. Dewalque (1868; 1880: 188, 438–443) listed most of the species introduced there, and revised the systematic position of several of them. Briart and Cornet (1870: 19, 33, 37) compared some of their species to Ryckholt's and adopted one of his names, *Natica mesostyle* (p. 27).

Because Ruhoff (1980) did not treat names of generic rank and Neave (1939–66) omitted many of Ryckholt's genera and incorrectly dated others, we list herein all of Ryckholt's nominal genera published in the *Mélanges*. Molluscan genera are listed first, then genera in other phyla. Two familial names are also included. The year of publication and the page or plate citation follow each name; available names are printed in boldface. Type species are indicated where known; if the author of a type species is not stated, that species was named by Ryckholt in the caption for the cited figures. Although we provide this list primarily to serve nomenclatural purposes, we include information on systematic position when such can be derived from the literature. We also state the geologic periods to which Ryckholt referred his taxa, but warn that some workers have considered the strata that Ryckholt called Cretaceous to be Tertiary (Dumont 1850; Dewalque 1879: 157; Holzapfel 1887: 38).

MOLLUSCA

Anomianella—1851, plate 10. Type species, by monotypy, *A. proteus*, figs. 21–23. Placed in Anomiidae (**Bivalvia**) by Vokes (1980: 59). **Carboniferous.**

Astreidomus—1860, plate 23. Type species, by monotypy, *A. biplicatus*, figs. 29, 30. A second species, *A. jantinopsis*, is named on plate 30, figures 26 and 27. **Gastropoda**, incertae sedis; similar in shape to *Melapium* (Olividae) and, superficially, to *Janthina* (Janthinidae). **Cretaceous.**

Dibaphus—1862, plate 35. Non *Dibaphus* Philippi, 1847 (Mitridae: Gastropoda). Type species, by monotypy, *D. cenomanicus*, figs. 15, 16. **Gastropoda**, incertae sedis. **Cretaceous.**

Dorsomya—1851, plate 10. Type species, by monotypy, *D. dorsata*, fig. 20. Placed in Myidae (**Bivalvia**) by Stoliczka (1871: 480); incertae sedis according to Vokes (1980: 215). **Carboniferous.**

Guildfortia—1862, plate 36. Type species, by monotypy, *G. prodromus*, figs. 23, 24. Placed in *Turbo* by Dewalque (1868, 1880: 441). Possibly an error for *Guildfordia* Gray 1850, Turbinidae (**Gastropoda**). **Cretaceous.**

Isoleda—1854, p. 164. A type species has not been designated. Woodward (1856: 473) says, "*Isoleda*, Ryck. 1856 [sic] = Leda solenoides . . . ," but falls short of designating a type. Ryckholt includes nine species (p. 165); only *Isoleda solenoides* (Goldfuss 1837) is illustrated (pl. 20, fig. 19). Woodward (1856: 473), Roemer (1876, pl. 24, fig. 3), and Beushausen (1895: 106) refer *Nucula solenoides* Goldfuss to *Cucullella* McCoy 1851, which McAlester (1969: N233) considered a synonym of *Nuculites* Conrad 1841 (Malletiidae: **Bivalvia**). Vokes (1980: 5) placed *Isoleda* in Nuculanidae. The systematic position of the genus will depend on the selection of a type species. **Silurian and Devonian.**

Lithariodomus—1860, plate 23. Type species, by monotypy, *L. siderotryus*, fig. 28. **Gastropoda**, incertae sedis. **Cretaceous.**

Naticodon—1851, page 75. Type species, by subsequent designation of Koninck (1881: 6), *Natica globosa* "Hoeninghaus." Knight (1941: 204) points out that *Natica globosa* Hoeninghaus 1830 is a nomen nudum validated by Ryckholt as *Naticodon globosum*. Ryckholt (1854: 197) placed *Naticodon* in the synonymy of *Naticopsis* McCoy in Griffith 1842 (Neritopsidae: **Gastropoda**), where it remains (Knight et al. 1960: I276). **Carboniferous** (See "Further notes" below.)

Omalia—1854, p. 72. Type species, by subsequent designation of Hind (1897: 129), *Modiola amygdalina* Phillips 1841 (Mytilacea: **Bivalvia**). **Devonian and Carboniferous.** (See "Further notes" below.)

Pheurotomaria—Plate 32. An error for *Pleurotomaria* Sowerby 1821; correctly spelled on Plate 31.

Phyllicocheilus—1861, plate 27. Type species, by monotypy, *P. morio*, figs. 25, 26. Dewalque (1868, 1880: 440) assigned *P. morio* to *Littorina* (Littorinidae: **Gastropoda**). **Cretaceous.**

Plerocera—Plate 35. An error for *Pterocera* Lamarck 1799; correctly spelled on Plate 34.

Prosopostoma—1862, plate 36. Six species are named in the genus; a type species has not been designated. Ryckholt's species resemble colombellinids and bursids (Strombacea and Tonnacea: **Gastropoda**). **Cretaceous.**

Rhealaria—1862, plates 33 and 34. Type species, by virtual tautonymy, *R. struthiolaria*, pl. 33, fig. 20. In the 1860's *Rhea* Brisson 1760 and *Struthio* Linné 1758 were both classified as members of the avian family Struthionidae, and members of both genera were referred to as ostriches (Parker 1866). Species of *Rhealaria* resemble colombellinids and struthiolariids (Strombacea: **Gastropoda**). **Cretaceous.**

Rhenana—1854, p. 28. Type species, by monotypy, *Sanguinolaria sulcata* Ryckholt 1854. Ryckholt proposed *Rhenana* for *Sanguinolaria sulcata* in the sense of Goldfuss 1840, not of Phillips 1836. According to ICZN Article 70c, this deliberate misapplication of the name creates the new nominal species *Rhenana sulcata* Ryckholt 1854. **Bivalvia,** incertae sedis. **Carboniferous.**

Scaldia—1851, plate 10. Type species, *S. lambotteana,* figs. 24–26, by subsequent designation of Stoliczka (1871: xviii) (misspelled as "*lambotheana*"). Chavan (1969: N514) placed *Scaldia* in the Fimbriidae **(Bivalvia). Carboniferous.**

Solenella—1851, plate 10. Non *Solenella* Sowerby 1833. A type species has not been designated. Ryckholt mentioned *Solenella* in the *Introduction* to Part 1 of the *Mélanges* (p. 17) and figured two species on plate 10. In the text corresponding to the plate, published in Part 2 (p. 55), Ryckholt synonymized *Solenella* with *Solenopsis* McCoy 1844. This name is preoccupied by *Solenopsis* Westwood 1840 and was replaced by *Solenomorpha* Cockerell 1903 (Grammysiidae: Pholadomyacea: **Bivalvia**) (Vokes 1980: 201). **Carboniferous.**

Torculina—1860, plate 23. Three species are named in the genus; a type species has not been designated. Dewalque (1868; 1880: 440) reassigned two of these species to *Turritella* (Turritellidae: **Gastropoda**). He did not mention the third species as it was not part of the fauna of the formation he was treating. **Cretaceous.**

Tornacia—1854, p. 77, 79. Introduced in the synonymy of *Dolabra* McCoy, 1844. **Bivalvia,** incertae sedis (Vokes 1980: 215). **Carboniferous.**

Tudicula—1862, plate 33. Non *Tudicula* H. & A. Adams 1864. Ryckholt's *Tudicula* is an emendation of *Tudicla* Röding 1798 (Turbinellidae: **Gastropoda**), as discussed below. **Cretaceous.**

OTHER PHYLA

Cirratulidae—1851, p. 29. Carus introduced the familial name "Cirratulida" based on *Cirratulus* Lamarck 1818 (Carus in Carus and Gerstaecker 1863: 441). Ryckholt's use of Cirratulidae antedates that of Carus. Polychaeta: **Annelida.**

Crateria—1854, p. 14. "Polypier," briefly described in a footnote, no species included. Anthozoa: **Coelenterata. Carboniferous.**

Nervia—1854, p. 15. A nomen nudum in **Brachiopoda.**

Planicrinus—1854, p. 15. Type species, by original designation, *Platycrinites granulatus* Miller 1821. Crinoidea: **Echinodermata. Carboniferous.**

Serpulidae—1851, p. 120. Ryckholt claimed authorship for the family name "Serpulidae," however, earlier names based on *Serpula* Linné 1758 include: Serpularia Rafinesque (1815: 136), Serpulées Lamarck (1818: 334, 357), Serpuleae Savigny (1822: 65), Serpulacea Brown (1837: 153) and Grube (1850: 333), and Serpulina MacLeay (1839: 699). Ryckholt's usage is thus a nomen correctum. Polychaeta: **Annelida.**

FURTHER NOTES

Naticopsis: The authorship of *Naticopsis* has been accepted as McCoy 1844 (Knight 1941: 205; Knight et al. 1960: 1276). However, in 1842 Griffith published a list of taxa that included many of the names that McCoy introduced in 1844. All of the new names in this list are nomina nuda, except for *Naticopsis,* which has eight available names listed in combination with it (pp. 19–20): *Natica ampliata, elliptica, elongata, lirata, planispira, plicistria,* and *tabulata,* all of Phillips 1836, and *Nerita spirata* Sowerby 1824. These combinations constitute an indication in the sense of ICZN Article 12(b)5; therefore *Naticopsis* McCoy in Griffith 1842 is available. Unfortunately, the type species designated by Meek and Worthen (1866: 364), *Naticopsis phillipsii* McCoy, was mentioned only as a nomen nudum by Griffith in 1842. McCoy described *N. phillipsii* in 1844; thus it is not one of the species originally included in *Naticopsis.* This circumstance renders the type designation by Meek and Worthen invalid. Waagen (1880: 100) and Koken (1889: 469) could be interpreted as regarding *Naticopsis canaliculata* McCoy as the type species, except it too was described in 1844. Knight (1933: 361), who accepted Meek and Worthen's designation, mentioned that some European workers had taken *Naticopsis ampliata* (Phillips) as the genotype of *Naticopsis.* The earliest such designation that we have found is that of Jakowlew (1899: 115), ". . . der als Typus die Gruppe *Naticopsis ampliata* Phill. . . . ." Recognition of *N. ampliata* instead of *N. phillipsii* as the type species of *Naticopsis* does not affect the systematic position of *Naticodon* Ryckholt; Knight (1941: 205) states, "*Naticopsis ampliata* . . . may well be a senior synonym of *N. globosum.*"

Omalia: Hind (1897: 129) considered the seventeen species originally included in *Omalia* to be a heterogeneous grouping. He took the first species listed, *Modiola amygdalina,* as the type, but several earlier authors (Woodward 1856: 471, Koninck 1885: 142, Fischer 1886: 976) give *Pullastra bistriata* Portlock 1843 as an example, as it is the only species of *Omalia* that Ryckholt figured (pl. 14, figs. 19, 20). Until Hind's type designation transferred *Omalia* to Mytilacea, it had been considered a section (Fischer 1886: 976) or synonym (Koninck 1885: 140) of *Parallelodon* Meek and Worthen 1866 (Parallelodontidae: Arcacea). Hind himself (1897: 129, 134) referred *P. bistriata* to *Parallelodon.* If an earlier designation making *Pullastra bistriata* the type species of *Omalia* were found, the systematic position of the genus would be greatly changed. In addition, *Omalia* would become a senior synonym for *Parallelodon,* assuming that *Pullastra bistriata* is indeed referable to it. Newell (1969: N865) considered *Omalia* to be a nomen oblitum of uncertain systematic position in the Bivalvia, but this does not qualify as rejection of the name according to ICZN Article 79(c)iv.

NOMENCLATURE OF *TUDICULA*

Ryckholt's use of *Tudicula* antedates that of H. & A. Adams (1864: 429) by two years; it is therefore necessary to determine the nomenclatural status of this name. *Tudicula* could be interpreted to be either a new generic name or a subsequent spelling of *Tudicla* Röding 1798, the type species of which is *Murex spirillus* Linné 1767 by subsequent designation of Angas (1878: 611). If *Tudicula* is a subsequent spelling, it could be either an emendation or a misspelling. In evaluating these possibilities, it is important to consider the historical confusion between *Tudicula* H. & A. Adams and *Tudicla* Röding.

Tudicula H. & A. Adams and *Tudicla* Röding are both currently regarded as members of the Turbinellidae (Gastropoda), although *Tudicla* is sometimes placed in its own family, Tudiclidae (Finlay and Marwick 1937: 39; Zinsmeister 1983: 1297). Many species of *Tudicla* have been incorrectly named as *Tudicula* a) because of the similarity of the names, b) because E. A. Smith (1884: 53), considering Röding's names to be unavailable, took *Tudicula* H. and A. Adams as a replacement name for *Tudicla,* and, most importantly, c) because Cossmann (1901: 68, 70) emended the spelling of *Tudicla* to *Tudicula*. Appendix A (below) lists eleven species that were incorrectly named by seven different authors as *Tudicula* rather than *Tudicla*. The confusion extends to the familial level as well. Cossmann (1901: 60) named the subfamily Tudiculinae of Turbinellidae, based on *Tudicla* Röding. This was emended to Tudiclidae by Finlay and Marwick (1937: 69) in translating it to familial status. *Tudicula* H. and A. Adams has not as yet been the basis of a family-group name.

These nomenclatural problems have obscured the evolutionary relationships of the taxa. For example, Zinsmeister (1983: 1297) was unaware that two lineages have been called "*Tudicula,*" saying, "The placement of *Tudicula* and *Vasum* by Wenz into the same family seems quite arbitrary and unwarranted because of fundamental morphological differences." In fact, *Tudicula* H. and A. Adams is anatomically similar to *Vasum* Röding 1798 (Vasinae: Turbinellidae) and more closely related to it than to *Tudicla* (Abbott 1959: 27, 32). There are no known fossil species of *Tudicula* and only six Recent species. In contrast, *Tudicla* Röding has an extensive fossil record dating from the Cretaceous. The only extant species is *Tudicla spirillus* (Linné 1767), the type of the genus. Clearly it is desirable to eliminate the nomenclatural confusion between these two lineages by replacing the name *Tudicula* H. & A. Adams.

The type specimens of Ryckholt's species of *Tudicula* have been lost (Dhont pers. comm.), but the figures of his *Tudicula amphinemalis* (pl. 33, fig. 9) and *T. tumulosa* (pl. 35, fig. 13) show that these taxa are either turbinellids or melongenids, genera of which were often conflated in classifications of the time. In addition, they resemble species placed in *Tudicla* Röding by contemporaneous authors such as Conrad (1860: 288), Gabb (1861: 141), and Meek (1864: 22, 23).

Although many of Röding's names were ignored until the 1900's (Dall 1906: 294; 1915: 1–4), Ryckholt probably knew of the name *Tudicla* because of its use by H. & A. Adams in *The Genera of the Recent Mollusca* (1853: 151) and by Chenu in *Manuel de Conchyliologie et de Paléontologie*

Conchyliologique (1859: 181). Ryckholt used two of the Adams' generic names, *Coralliophila* (1853: 135) and *Forskalia* (1854: 432), in Part 3 of the *Mélanges* (1861, pls. 29 and 30), so he was familiar with their treatise. Ryckholt knew of Chenu's *Manuel,* as he cited it in two papers that he published in *Journal de Conchyliologie* (1860a: 181; 1860b: 185, 188). Stoliczka (1867: 150) states that *Tudicla* "[had] become familiar in the paleontological literature," especially "through Adams' and Chenu's conchological works." Ryckholt might also have known of Röding's work from Fischer's bibliographic notice of it in the *Journal* (1858), or from Herrmannsen's notice (1853) of the availability of generic names in Link (1807), who used some of Röding's names. In particular, Herrmannsen (p. 231) cites "*Tudicla,* Link, 1807, *l.c.* iii. p. 120. (*Tudicla,* Bolt. emend.)." Röding's names were often of uncertain status as some workers in the 1800's and early 1900's considered Röding's work, *Museum Boltenianum,* to be an auction catalogue and thus unavailable. In 1926 the ICZN confirmed Röding's work as available for zoological nomenclature (Opinion 96).

Because Ryckholt had opportunity to know of *Tudicla* Röding, we deem *Tudicula* Ryckholt to be a subsequent spelling of *Tudicla,* rather than a new name. According to ICZN Article 33, this subsequent spelling is either an emendation, defined as a "demonstrably intentional change in the original spelling of a name," or a misspelling (an incorrect subsequent spelling). A sufficient condition for a subsequent spelling to be interpreted as "demonstrably intentional" occurs "when two or more names in the same work are treated in a similar way." Ryckholt's use satisfies this condition, for the spelling "*Tudicula*" appears twice in the third part of the *Mélanges,* in the combinations *Tudicula amphinemalis* and *Tudicula tumulosa* on plates 33 and 35, respectively. The spelling "*Tudicla*" does not appear. Plates 33 and 35 were issued with a three-month interval, and *Tudicula* is not mentioned on the errata page; we therefore deem the spelling to be intentional: it is an emendation of *Tudicla* Röding, not a misspelling. That Ryckholt would emend *Tudicla* is not surprising. He had the requisite linguistic knowledge, as shown by the imaginative names that he chose for his taxa and by his having published a treatise on languages (1868). He might have been encouraged by Herrmannsen's speculation (1849: 635) that the name is derived from the Latin *tudicula.* Regardless of whether *Tudicula* Ryckholt is a newly introduced name or an emendation of an existing one, it enters into the literature and into homonymy.

Although there are etymological reasons for emending *Tudicla,* there is no clear evidence in Röding's text (1798: 145), as required by ICZN Article 32(c)ii, that *Tudicla* is an incorrect original spelling. Furthermore, Dodge (1957: 157) demonstrates that *Tudicla* is a syncopated form of and an acceptable spelling for the Latin word "*tudicula.*" *Tudicla* is thus a correct original spelling and must be preserved unaltered (Article 32b). Ryckholt's emendation is therefore unjustified, as is Cossmann's (1901: 68, 70). These emendations create the nominal taxa *Tudicula* Ryckholt 1862 and *Tudicula* Cossmann 1901, which are junior objective synonyms of *Tudicla* Röding 1798 according to Article 33(b)iii.

Because *Tudicula* H. & A. Adams 1864 is in current use, and is a junior homonym of *Tudicula* Ryckholt 1862, we propose the following new name in accordance with ICZN Article 60, which states that a junior homonym of an available name *must* be replaced (our emphasis).

Tudivasum nom. nov. pro *Tudicula* H. & A. Adams 1864

Tudicula H. & A. Adams 1864, Proceedings of the

Zoological Society of London for 1863, p. 429. Non *Tudicula* Ryckholt 1862 nec *Tudicula* Cossmann 1901. Type, by subsequent designation of Wenz (1943: 1303), *Tudicla armigera* A. Adams 1856.

Etymology: *Tudi-* + *vasum*, neuter, from the genera *Tudicula* and *Vasum*, to reflect the relationship of the genus to *Vasum* Röding. The generic names are derived from the Latin *tudicula*, an instrument for pressing olives, which is the diminutive of *tudes*, a hammer, and *vas* or *vasum*, a vase or vessel.

The replacement of *Tudicula* by *Tudivasum* results in the following new combinations for the six nominal taxa referable to the group. The original combination follows each citation.

Tudivasum armigerum (A. Adams 1856), p. 221; *Tudicla armigera*.
Tudivasum inerme (Angas 1878), p. 610, 2 figs.; *Tudicula inermis*.
Tudivasum kurtzi (Macpherson 1964), pp. 209–210, 1 pl.; *Tudicula (Tudicula) kurtzi*.
Tudivasum rasilistoma (Abbott 1959), p. 29, pl. 10; *Tudicula rasilistoma*.
Tudivasum spinosum (H. & A. Adams 1864), p. 429; *Tudicla (Tudicula) spinosa*.
Tudivasum zanzibaricum (Abbott 1958), pp. 1–4, figs. 1–7; *Tudicula zanzibarica*.

Also referable to *Tudivasum* is an unidentified *Tudicula* that Cochran (1986: 1) reported from Tasmania. Abbott (1959: 27) referred *Tudicla sinotecta* Ludbrook 1941 to *Tudicula*, but Ludbrook (p. 97, pl. 5, fig. 14) describes his species as having one columellar fold. *Tudicula* have three or four such folds (among other differences); *T. sinotecta* therefore should remain in *Tudicla*.

APPENDIX A

The following nominal species were erroneously described as *Tudicula* rather than *Tudicla* as judged by their authors' (1) attributing the generic name to Röding, Bolten, or Link, (2) referring to *T. spirillus* as the type of the genus, (3) stating that the generic name was emended or used in Cossmann's sense, (4) comparing the species to *T. spirillus*, or (5) mentioning the presence of a single columellar plication. This list, which is not intended to be comprehensive, was compiled by examining the original descriptions of all nominal species of *Tudicula* and *Tudicla* listed in the Zoological Record or mentioned in the works cited in this paper.

aegyptiaca Mayer-Eymar 1895, pp. 45–46, pl. 2, fig. 5.
alta Wilckens 1922, p. 20, pl. 4, figs. 7–11.
angulata Tate 1888, pp. 160–161, pl. 10, fig. 9.
bispinosa Grabau 1907, p. 619, pl. 1, figs. 1, 3, 4.
costata Tate 1888, pp. 159–160, pl. 10, fig. 8.
hourcqi Collignon 1951, p. 119, pl. 19(7), figs. 2, 2a.
ishiii Matsui 1959, p. 298, pl. 2, fig. 4.
secans Mayer-Eymar 1895, p. 47.
sulcata Marshall 1917, p. 455, pl. 35, fig. 19.
turbinata Tate 1888, p. 160, pl. 10, fig. 7.
umbilicaris Mayer-Eymar 1895, pp. 46–47, pl. 2, fig. 6.

ACKNOWLEDGMENTS

We express our appreciation to Dr. Annie V. Dhont, Institut Royal des Sciences Naturelles de Belgique, Brussels, and Mr. John Cooper and Dr. R. J. Cleveley, British Museum (Natural History), London, for correspondence and comments concerning Ryckholt and his publications. We also thank Dr. Carol C. Jones, Vassar College, Poughkeepsie, New York, and Drs. Kenneth J. Boss and Ruth D. Turner, Museum of Comparative Zoology, Cambridge, for reading this paper and making suggestions for its improvement, and Drs. F. M. Bayer and C. W. Sabrosky, National Museum of Natural History, Washington, DC, for discussing the interpretation of parts of the International Code of Zoological Nomenclature.

LITERATURE CITED

ABBOTT, R. T. 1958. A new Recent species of *Tudicula* from Zanzibar (Gastropoda: Vasidae). Notulae Naturae of The Academy of Natural Sciences of Philadelphia. No. 305, 4 pp.

———. 1959. The family Vasidae in the Indo-Pacific. Indo-Pacific Mollusca 1: 15–32.

ADAMS, A. 1856. Descriptions of twenty-five new species of shells from the collection of Hugh Cuming, Esq. Proceedings of the Zoological Society of London for 1855, pp. 221–226.

ADAMS, H., AND A. ADAMS. 1853–1854. The genera of the Recent Mollusca, arranged according to their organization. Vol. 1. John van Voorst, London. Pp. 1–256, pls. 1–32 (1853), pp. 257–484, pls. 33–60 (1854).

ADAMS, H. 1864. Descriptions of new species of shells, chiefly from the Cumingian collection. Proceedings of the Zoological Society of London for 1863, pp. 428–435.

ANGAS, G. F. 1878. Description of a new species of *Tudicula*. Proceedings of the Zoological Society of London for 1878, pp. 610–611.

BEUSHAUSEN, L. 1895. Die Lamellibranchiaten des rheinischen Devon mit Ausschluss der Aviculiden. Abhandlungen der Königlich Preussischen geologischen Landesanstalt, Neue Folge 17, 514 pp., 38 pls.

BRIART, A. AND F. L. CORNET. 1870. Description minéralogique, géologique et paléontologique de la Meule de Bracquegnies. Mémoires Couronnés et Mémoires des Savants Étrangers, Académie Royale des Sciences de Belgique 34, 92 pp., 8 pls.

——— AND ———. 1871. Description des fossiles du Calcaire Grossier de Mons. Première Partie. Gastéropodes. Ordre I.—Prosobranches. Section A.—Siphonostomes. Mémoires Couronnés et Mémoires des Savants Étrangers, Académie Royale des Sciences de Belgique 36, viii + 76 pp., 5 pls.

BRISSON, M. J. 1760. Ornithologie ou méthode contenant la division des oiseaux . . . . Vol. 5. Cl. Jean-Baptiste, Paris. [iv+] 544 + lvi pp., 42 pls.

BROWN, T. 1837. The conchologist's text-book, embracing the arrangements of Lamarck and Linnaeus, with a glossary of technical terms. Archibald Fullarton & Co., Glasgow. 180 pp., 19 pls.

CARUS, J. V. AND C. E. A. GERSTAECKER. 1863. Handbuch der Zoologie. Zweiter Band. Verlag von Wilhelm Engelmann, Leipzig. vii + 642 pp.

CHAVAN, A. 1969. Superfamily Lucinacea Fleming, 1828. Pages N491–N518 *in* R. C. Moore, ed. Treatise on invertebrate paleontology. Part N, vol. 2, Mollusca 6, Bivalvia. Geological Society of America.

CHENU, J. C. 1859. Manuel de conchyliologie et de paléontologie conchyliologique. Vol. 1. Libraire Victor Mason, Paris. vii + 508 pp.

CLEEVELY, R. J. 1983. World palaeontological collections. British Museum (Natural History), London. 365 pp.

COCHRAN, T. 1986. Tasmanian *Tudicula*! Australian Shell News 54: 1.

COCKERELL, T. D. A. 1903. The name Solenopsis. Nature 67: 559.

COLLIGNON, M. 1951. Le Crétacé Supérieur d'Antonibe. Couches de passage du Crétacé au Tertiare. Annales Géologiques du Service des Mines (Madagascar) 19: 73–184, pls. 13(1)–20(8).

CONRAD, T. A. 1841. Fifth annual report on the palaeontology of the state of New York. State of New York [Geological Survey], [reports to] Assembly, No. 150 [of the legislature], pp. 25–57.

———. 1860. Descriptions of new species of Cretaceous and Eocene fossils of Mississippi and Alabama. Journal of The Academy of Natural Sciences of Philadelphia (2)4: 275–298, pls. 46–47.

COSSMANN, M. 1901. Essais de paléoconchologie comparée. Vol. 4. Société d'Editions Scientifiques, Paris. [iv+] 293 pp., 10 pls.

COX, L. R. 1925. The fauna of the basal shell-bed of the Portland Stone, Isle of Portland. Proceedings of the Dorset Natural History and Antiquarian Field Club 46: 113–172, 5 pls.

CROSSE, H. 1863. Mélanges paléontologiques, par le baron P. de Ryckholt, lieutenant-colonel d'artillerie, chevalier de l'ordre de Léopold.–Deuxième et troisième parties. Journal de Conchyliologie 11: 216–219.

DALL, W. H. 1906. Early history of the generic name Fusus. Journal of Conchology 11: 289–297.

———. 1915. An Index to the Museum Boltenianum. Smithsonian Institution Publication 2360, 64 pp.

DEWALQUE, G. 1868. Prodrome d'une description géologique de la Belgique. Bruxelles. viii + 442 pp. [Not seen]

———. 1879. Revue des fossiles Landeniens décrits par de Ryckholt. Annales de la Société Géologique de Belgique 6: 156–167.

———. 1880. Prodrome d'une description géologique de la Belgique. Seconde édition, conforme à la première. H. Manceaux, Bruxelles. xi + 501 pp.

DODGE, H. 1957. A historical review of the mollusks of Linnaeus. Pt. 5. The genus *Murex* of the class Gastropoda. Bulletin of the American Museum of Natural History 113: 73–224.

DUMONT, A. H. 1850. Rapport de M. Dumont sur le mémoire intitulé: *Mélanges Paléontologiques;* par M. P. de Ryckholt. Bulletin de l'Académie Royale des Sciences de Belgique 17(2): 314–317.

——— AND J. F. CANTRAINE. 1848. Rapport sur le mémoire intitulé: Élucubrations Paléontologiques, par M. le baron de Ryckholdt. Bulletin de l'Académie Royale des Sciences de Belgique 15(1): 6–9.

FINLAY, H. J. AND J. MARWICK. 1937. The Wangaloan and associated molluscan faunas of Kaitangata-Green Island Subdivision. New Zealand Geological Survey Paleontological Bulletin 15: 1–140.

Fischer, P. 1858. Curiosités bibliographiques. Museum Boltenianum. Journal de Conchyliologie 7: 206–208.

———. 1886. Manuel de conchyliologie et de paléontologie conchyliologique. Fascicule 10. Libraire F. Savy, Paris. pp. 897–1008.

Fritsch, A. 1910. Miscellanea paleontologica II. Mesozoica. Selbsverlag, Prag. 26 pp., 10 pls.

Gabb, W. M. 1861. Synopsis of the Mollusca of the Cretaceous Formation, including the geographical and stratigraphical range and synonymy. Proceedings of the American Philosophical Society 8: 57–257.

Goldfuss, A. 1837–1840. Petrefacta Germaniae . . . Abbildungen und Beschreibungen der Petrefacten Deutschlands und der angränzenden Länder, ... Arnz & Comp., Düsseldorf. 2(6): 141–224, pls. 122–146 (1837); 2(7): 225–312, pls. 147–165 (1840).

Grabau, A. W. 1907. Studies of Gastropoda. III. On orthogenetic variation in Gastropoda. American Naturalist 41: 607–646, pls. 1–3.

Gray, J. E. 1850. Explanation of the plates. Vol. 4 *in* M. E. Gray. Figures of molluscous animals, selected from various authors, etched for the use of Students. London. iv + 219 pp.

Griffith, R. J. 1842. Notice respecting the fossils of the mountain limestone of Ireland as compared with those of Great Britain, and also with the Devonian System. Dublin. 25 pp., 1 pl.

Grube, A. E. 1850. Die Familien der Anneliden. Archiv für Naturgeschichte 16(1): 249–364.

Hermann, A. 1900. Catalogue d'ouvrages d'occasion sur la conchyliologie et la paléoconchyliologie voyages scientifiques faunes, etc., provenant en partie de la vente de M. H. Crosse, Directeur du *Journal de Conchyliologie*. Catalogue No. 66, Librairie Scientifique A. Hermann, Editeur, Paris. 36 pp.

Herrmannsen, A. N. 1849. Indicis generum malacozoorum primordia. Vol. 2. Theodori Fischeri, Cassellis. Pp. 493–717.

———. 1853. On some genera of shells, established in 1807 by the late H. F. Link. Proceedings of the Zoological Society of London 19: 228–233.

Hind, W. 1897. A Monograph of the British Carboniferous Lamellibranchiata. Vol. 1, Part II. Mytilidae, Arcidae, Nuculidae. Palaeontographical Society, London. Pp. 81–208, pls. 3–15.

Hoeninghaus, F. W. 1830. Versuch einer geognostichen Eintheilung seiner Versteinerung-Sammlung, nach Berathung der Herren Brongniart, Goldfuss, Bronn, Cordier, Hausmann, von Leonhard, Noeggerath und Delabêche's Karte. (Erster Theil). Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 1: 226–245.

Holzapfel, E. 1887. Die Mollusken der Aachener Kreide [Erste Lieferung]. Palaeontographica 34: 29–72, pls. 4–5.

International Commission on Zoological Nomenclature. 1926. Opinion 96. Museum Boltenianum. Smithsonian Miscellaneous Collections 73(4): 16–18.

———. 1985. International code of zoological nomenclature, third edition, adopted by the XX General Assembly of the International Union of Biological Sciences, London. xx + 338 pp.

Jakowlew, N. 1899. Die Fauna einiger oberpalaeozoischer Ablagerungen Russlands. I. Die Cephalopoden und Gastropoden. Mémoires du Comité Géologique (St. Petersburg) 15(3): 81–140, 5 pls.

Knight, J. B. 1933. The gastropods of the St. Louis, Missouri, Pennsylvanian Outlier: VI. The Neritidae. Journal of Paleontology 7: 359–392, pls. 40–46.

———. 1941. Paleozoic gastropod genotypes. Geological Society of America Special Papers Number 32, vi + 510 pp., 96 pls.

———, L. R. Cox, A. M. Keen, R. L. Batten, E. L. Yochelson, and R. Robertson. 1960. Systematic descriptions [Archaeogastropoda]. Pages 1169–1310 *in* R. C. Moore, ed. Treatise on invertebrate paleontology. Part I, Mollusca 1. Geological Society of America.

Koken, E. 1889. Ueber die Entwickelung der Gastropoden vom Cambrium bis zur Trias. Neues Jahrbuch für Mineralogie, Geologie und Palaeontologie. 6. Beilage-Band. Pp. 305–484, pls. 10–14.

Koninck, L. G. de. 1881. Faune du Calcaire Carbonifère de la Belgique, Part 3. Gasteropodes. Musée Royal d'Histoire Naturelle de Belgique, Annales 6, 170 pp., 21 pls.

———. 1885. Faune du Calcaire Carbonifère de la Belgique, Part 5. Lamellibranches. Musée Royal d'Histoire Naturelle de Belgique, Annales 11, 283 pp., 41 pls.

Lamarck, J. B. P. A. 1799. Prodrome d'une nouvelle classification des coquilles, ... Mémoires de la Société d'Histoire Naturelle de Paris [1]: 63–91, fold-out table.

———. 1818. Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, ... Vol. 5. Deterville, also Verdiere, Paris. [iv+] 612 pp.

Link, H. F. 1807. Beschreibung der Naturalien-Sammlung der Universität zu Rostock. Dritte Abtheilung. Adlers Erben, Rostock. Pp. 101–160. [Reprinted 1931]

Linné, C. von. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio Decima, Reformata. Laurentii Salvii, Holmiae. iv + 824 pp.

———. 1767. Systema Naturae, Tom. I. Pars II. Edition Duodecima Reformata, Laur. Salvii, Holmiae. Pp. 533–1328 [+38].

LUDBROOK, N. H. 1941. Gastropoda from the Abattoirs Bore, Adelaide, South Australia together with a list of some miscellaneous fossils from the bore. Transactions of the Royal Society of South Australia 65: 79–102, pls. 4–5.

MACLEAY, W. S. 1839. Note on the Annelida. Pages 699–701 *in* R. I. Murchison. The Silurian System, founded on geological researches . . . . Part 2. John Murray, London.

MACPHERSON, J. H. 1964. A new species of *Tudicula* from North Australia. Memoirs of the National Museum of Victoria No. 26, pp. 209–210, 1 pl.

MARSHALL, P. 1917. The Wangaloa Beds. Transactions and Proceedings of the New Zealand Institute for 1916, 49: 450–460, pls. 34–37.

MATSUI, M. 1959. On some Oligocene molluscan fossils from Hokkaido, Japan. Journal of the Faculty of Science Hokkaido University, Series 4. Geology and Mineralogy 10: 289–304, pls. 1–2.

MAYER-EYMAR, C. 1895. Descriptions de coquilles fossiles des terrains tertiaires inférieurs (suite). Journal de Conchyliologie 43: 40–54, pls. 2–4.

MCALESTER, A. L. 1969. Family Malletiidae Adams & Adams, 1858. Pages N231–N235 *in* R. C. Moore, ed. Treatise on invertebrate paleontology. Part N, vol. 1, Mollusca 6, Bivalvia. Geological Society of America.

MCCOY, F. 1844. A Synopsis of the characters of the Carboniferous limestone fossils of Ireland. University Press, Dublin. viii + 207 pp., 29 pls.

———. 1851. On some new Silurian Mollusca. Annals and Magazine of Natural History (2)7: 45–63.

MEEK, F. B. 1864. Check List of the invertebrate fossils of North America. Cretaceous and Jurassic. Smithsonian Miscellaneous Collection 177: 1–40.

——— AND A. H. WORTHEN. 1866. Descriptions of invertebrates from the Carboniferous System. Geological Survey of Illinois, vol. 2, Palaeontology, Section 2, pp. 145–411, pls. 14–20, 23–32.

MILLER, J. S. 1821. A natural history of the Crinoidea, or lily-shaped animals; . . . . C. Frost, Broadstreet, Bristol. viii + 150 pp., 50 pls., frontispiece.

MOURLON, M. 1881. Géologie de la Belgique. Vol. 2. F. Hayez, Brussels. 392 pp.

NEAVE, S. A., ed. 1939–1966. Nomenclator Zoologicus. Zoological Society of London, London. 6 vols. 1: xiv + 957 pp., 1939; 2: [iv+] 1025 pp., 1939; 3: [iv+] 1065 pp., 1940; 4: [iv+] 758 pp., 1940; 5: [viii+] 308 pp., 1950; 6: [xii+] 329 pp., 1966 (vol. 6 ed. by M. A. Edwards and A. T. Hopwood).

NEWELL, N. D. 1969. Pages N863–N867 *in* Class, Order, and Family Uncertain, *in* R. C. Moore, ed. Treatise on invertebrate paleontology. Part N, Mollusca 6(2), Bivalvia. Geological Society of America.

PARKER, W. K. 1866. On the structure and development of the skull in the ostrich tribe. Philosophical Transactions of the Royal Society of London 156: 113–183, pls. 7–15.

PHILIPPI, R. A. 1847. Beschreibung zweier neuer Conchyliengeschlecter, Dibaphus und Amphichaena, nebst einigen Bemerkungen über Cyamium, Ervilia und Entodesma. Archiv für Naturgeschichte 13(1): 61–66, pl. 3.

PHILLIPS, J. 1836. Illustrations of the geology of Yorkshire. . . . Part II. The mountain limestone district. John Murray, London. xx + 254 pp., 25 pls.

———. 1841. Figures and descriptions of the Paleozoic fossils of Cornwall, Devon, and West Somerset; . . . . Longman, Brown, Green, & Longmans, London. xii + 231 pp., 60 pls.

PORTLOCK, J. E. 1843. Report on the geology of the county of Londonderry, and of parts of Tyrone and Fermanagh. Her Majesty's Stationary Office, Dublin. xxxii + 784 pp., 44 pls., 9 fold-out pls., 1 fold-out map.

RAFINESQUE, C. S. 1815. Analyse de la nature ou tableau de l'univers et *des corps organisés*. Palerme. 224 pp.

RIDDER, A. DE. 1928. La crise de la neutralité Belge de 1848. Le dossier diplomatique. M. Weissenbruch, Bruxelles. Vol. 1, xxxxv + 394 pp.; vol. 2, 329 pp.

RÖDING, P. F. 1798. Museum Boltenianum sive catalogus cimeliorum, pars secunda. Johan. Christi. Trappii., Hamburg. vii + 199 pp. [Reprinted 1906, 1986]

ROEMER, F. VON. 1876. Lethaea Palaeozoica. Atlas. 62 pls. *in* Lethaea Geognostica 1(1). E. Schweizerbart'sche Verlagshandlung, Stuttgart.

ROLLIER, L. 1923. Rectification de nomenclature. Revue Critique de Paléozoologie et de Paléophytologie 27: 67.

RUHOFF, F. A. 1980. Index to the species of Mollusca introduced from 1850 to 1870. Smithsonian Contributions to Zoology 294: 1–640.

RYCKHOLT, P. DE. 1845. Résumé géologique sur le genre *Chiton* Lin. Bulletin de la Académie Royale des Sciences et Belles-Lettres de Bruxelles 12(2): 36–62, 4 pls.

———. 1851–1862. Mélanges Paléontologiques. (See collation ante)

———. 1852. Notice sur les genres: *Nautilus*, Breyn, *Vestinautilus, Asymptoceras, Coya,* de Ryckholt, et *Terebrirostra,* d'Orbigny. Bruxelles. 10 pp., 1 pl.

———. 1860a. Quelques mots à propos du *Truncatella dubiosa,* Adams. Journal de Conchyliologie 8: 181–182.

———. 1860b. Revue des genres qui composent la famille des Haliotidae, d'Orbigny. Journal de Conchyliologie 8: 183–188.

———. 1862a. Déductions paléontologiques appliquées à la conchyliologie de notre époque. Journal de Conchyliologie 10: 28–35.

———. 1862b. Description de deux Tuniciers carbonifères et d'un nouveau genre de la famille des Chitonidae. Journal de Conchyliologie 10: 255–260, pl. 12.

———. 1862c. Notice sur le genre *Craspedotus.* Journal de Conchyliologie 10: 410–417.

———. 1868. La Province de Liége. Les cinq Gaules, l'Italie, la Grèce, etc. et le Flamand, langue primordiale, mère de toutes les langues. Pt. 1. Liége. [Not seen; cited from the British Library General Catalogue of Printed Books to 1975, 286: 152 (1985)]

Ryckman de Betz, [F.] de. 1957. Armorial Général de la Noblesse Belge. H. Dessain, Liège. xv + 814 pp.

Savigny, J. C. 1822. Système des Annelides principalement de celles des côtes de l'Egypte et de la Syrie. . . . Imprimerie Impériale, Paris. 128 pp.

Smith, E. A. 1884. Mollusca. Pages 34–116, pls. 4–7 *in* Report on the zoological collections made in the Indo-Pacific Ocean during the voyage of H. M. S. 'Alert' 1881–2. Pt. I. The collections from Melanesia. Trustees [British Museum], London.

Sowerby, G. B. 1833. [Genus *Solenella.*] Proceedings of the Committee of Science and Correspondence of the Zoological Society of London 2: 197.

Sowerby, J. 1821. The mineral conchology of Great Britain; . . . . W. Arding, London. Vol. 3, pp. 127–194, pls. 272–306.

Sowerby, J. D. C. 1824. The mineral conchology of Great Britain; . . . . W. Arding, London. Vol. 5, pp. 65–138, pls. 444–495.

Stoliczka, F. 1867. The Gastropoda. Memoirs of the Geological Society of India, Paleontologica Indica, Cretaceous Fauna of Southern India, vol. 2, pts. 1–4, pp. 1–204, pls. 1–16.

———. 1870–1871. The Pelecypoda, with a review of all known genera of this class, fossil and recent. Memoirs of the Geological Society of India, Paleontologica Indica, Cretaceous Fauna of Southern India, vol. 3, xxii + 537 pp., 50 pls.

Tate, R. 1888. The gastropods of the older Tertiary of Australia. Transactions of the Royal Society of South Australia 10: 91–176, pls. 1–13.

Ubaghs, [J.] C. 1879. Description géologique et paléontologique du sol du Limbourg, avec catalogue général des fossiles du terrain crétacé . . . . Ruremonde. 275 pp., 8 pls.

Vokes, H. E. 1980. Genera of the Bivalvia: A systematic and bibliographic catalogue (revised and updated). Paleontological Research Institution, Ithaca, New York. xxvii + 307 pp.

Waagen, W. 1880. Salt-range fossils. I. Productus-limestone fossils. 2. Pisces-Cephalopoda: Supplement. Gasteropoda. Memoirs of the Geological Society of India, Paleontologica Indica, Ser. 13, pp. 73–183, pls. 7–16.

Wenz, W. 1943. Gastropoda: Allgemeiner Teil und Prosobranchia. Pages 1201–1506 *in* O. H. Schindewolf, ed.. Handbuch der Paläozoologie. Band 6(1), Lieferung 8. Verlag von Gebrüder Borntraeger, Berlin.

Westwood, J. O. 1840. Observations on the genus *Typhlopone,* with descriptions of several exotic species of ants. Annals and Magazine of Natural History 6: 81–89, pl. 2.

Wilckens, O. 1922. The Upper Cretaceous gastropods of New Zealand. New Zealand Geological Survey Palaeontological Bulletin 9, viii + 42 pp., 5 pls., 1 fold-out map.

Woodward, B. B. 1913. Catalogue of the books, manuscripts, maps and drawings in the British Museum (Natural History). London. vol. 4, pp. 1495–1956.

Woodward, S. B. 1856. A manual of the Mollusca; or, rudimentary treatise of recent and fossil shells. John Weale, London. Pt. 3, pp. 331–486.

Zinsmeister, W. J. 1983. New Late Paleocene molluscs from the Simi Hills, Ventura County, California. Journal of Paleontology 57: 1282–1303.

Proceedings of The Academy of Natural Sciences of Philadelphia 139: 65–85, 1987.

Two New Species of Pygmy Sunfishes (Elassomatidae, *Elassoma*) from the Carolinas

FRED C. ROHDE AND RUDOLF G. ARNDT
North Carolina Division of Marine Fisheries
7225 Wrightsville Ave., Wilmington, NC 28403
and
Faculty of Natural Sciences and Mathematics
Stockton State College, Pomona, NJ 08240

ABSTRACT.—Two new similar-appearing species of pygmy sunfishes, *Elassoma boehlkei* and *E. okatie*, are described from the Coastal Plain of North Carolina and South Carolina. *Elassoma boehlkei* is distinguished primarily by its mode of 13 dark and narrow trunk bars (mean 0.57 mm in width), a wide interbar space, several morphometric measurements, and by its relatively small size. *Elassoma okatie* is characterized by a mode of 11 dark and wide trunk bars (mean 1.11 mm in width), a narrow interbar space, several morphometric measurements, and by its larger size. The only other barred pygmy sunfish, *E. zonatum*, has a mode of nine dark and wide trunk bars, and its dark shoulder blotch and dark postocular stripe are both lacking in the two new species. *Elassoma boehlkei* occurs in two areas in the upper and lower Waccamaw River drainage, and at one site in the Santee River drainage. *Elassoma okatie* is known from the Edisto, New, and Savannah river drainages. Most populations of both new species occur in man-disturbed habitats. All sites for both species are characterized by shallow and quiet water, a soft detritus-rich substrate, and abundant emergent and/or submerged aquatic vegetation. A key is given to the species of *Elassoma*. [*Elassoma*, fishes, new species, North Carolina, pygmy sunfishes, South Carolina, systematics]

The genus *Elassoma* contains six known species: *E. zonatum* Jordan, *E. evergladei* Jordan, *E. okefenokee* Böhlke, the two new species described herein, and one additional undescribed species being described by others. The genus is found throughout much of the Atlantic and Gulf coastal plains of the United States and in the Mississippi River Valley north to Illinois. *Elassoma zonatum*, the banded pygmy sunfish, is the most widely distributed form, and its range is essentially that of the genus. *Elassoma evergladei*, the Everglades pygmy sunfish, occurs from North Carolina through much of peninsular Florida and into southern Alabama. *Elassoma okefenokee*, the Okefenokee pygmy sunfish, is restricted to southern Georgia and the northern half of Florida. Böhlke and Rohde (1980) give distribution maps for the three previously described species. The two species described here have limited distributions in North Carolina and South Carolina and are sympatric with *E. zonatum* and *E. evergladei*. The remaining undescribed *Elassoma*, the spring pygmy sunfish, is known from one spring in northern Alabama, although it formerly occurred in two others (Mettee and Ramsey 1986). Relationships among the six species will be discussed in a future paper.

Both species described herein were first collected in the 1950s (by Warren J. Houck of Cornell University in 1950 and by Harry W. Freeman of the College of Charleston in 1955) but were not then recognized as new. In 1969, Edward F. Menhinick collected additional material of one of these species in southeastern North Carolina and brought it to the attention of James E. Böhlke, Curator of Ichthyology, ANSP. Subsequent examination of museum specimens by Böhlke and the senior author uncovered the 1955 collection of this species, and what appeared to be yet another undescribed *Elassoma*. Field collections by the authors confirmed the presence of the second new form. Unfortunately, the death of Dr. Böhlke prevented his participation as an author of this paper.

Our placement of the pygmy sunfishes in the family Elassomatidae, rather than in the Centrarchidae, follows Branson and Moore (1962), Roberts (1964), Mettee (1974), Avise et al. (1977), and Johnson (1984). Their data on the behavioral, biochemical, osteological, and sensory relationships among the currently-recognized forms of the family Centrarchidae strongly suggest that *Elassoma* is so specialized and divergent from the centrarchids to warrant placement in a separate family. Johnson (1984) even suggests that the Elassomatidae is not closely related to the Centrarchidae.

METHODS

Counts and measurements follow Hubbs and Lagler (1958), except that all rays in the dorsal and anal fins were counted, i.e. the elements of the last ray, if split into two, were counted as two. Vertebrae counts, fin-spine counts, and fin-ray counts were made from radiographs. Specimens were cleared and stained to examine dentition. A frequency description expressed as (16)17–20(21) indicates that at least 90% of the counts are between 17 and 20 inclusive, with extremes of 16 and 21. Body length is standard length (SL) in millimeters (mm). Body measurements were made with a dial caliper. All dark bars on the trunk between the pectoral fin insertion and the caudal fin base were counted. Bar width and the distance between bars was measured on the midline of the side with an ocular micrometer and a ratio of dark to light bar width was calculated.

In addition to specimens examined for the data above (sample sizes in tables), dozens of additional specimens were collected and superficially examined for color, color patterns, size, and sexual dimorphism. The two new species are compared to specimens of the other barred pygmy sunfish, *E. zonatum*, from North Carolina and South Carolina.

Color descriptions are from live and preserved individuals, 35 mm color transparencies, and color prints. Specimens were drawn from 35 mm color transparencies.

Localities for both new species were sampled frequently (frequency in Results) from 1975 to 1986, except for one recently-discovered locality sampled only once. Most sites were sampled in all seasons, usually with a 3 m × 1.2 m × 3.2 mm-mesh seine, and under a range of weather. Usually recorded were water depth, current, and flow; substrate; air and water temperature; pH; conspicuous aquatic and nearby terrestrial plants; and fish species-associates.

Institutions referred to herein are: ANSP, Academy of Natural Sciences of Philadelphia; AU, Auburn University; CU, Cornell University; GMBL, Grice Marine Biological Laboratory; MCZ, Museum of Comparative Zoology, Harvard University; NCSM, North Carolina State Museum of Natural History; RC, Roanoke College; TU, Tulane University; UMMZ, University of Michigan Museum of Zoology; UF, Florida State Museum; UNC, University of North Carolina; UNCC, University of North Carolina at Charlotte; UNCW, University of North Carolina at Wilmington; UNO, University of New Orleans; and USNM, United States National Museum.

Elassoma boehlkei n. sp., Carolina pygmy sunfish, Figs. 1a and 1b, Tables 1–5

Elassoma n. sp. Menhinick et al. 1974. Undescribed species from Juniper Creek.

Holotype. ANSP 158481, 22.10 mm SL, adult male, Waccamaw River Drainage, North Carolina, Brunswick County, Juniper Creek at State Route 1340 bridge, 1.6 km E Makatoka and 17.8 km NW Supply, 13 Mar 1983, Rohde.

Paratypes. WACCAMAW RIVER DRAINAGE: NORTH CAROLINA: Brunswick Co.: ANSP 158482, 25 specimens (17.20–24.60 mm), same collection data as holotype; UMMZ 213588, 10 (16.00–21.50 mm) and TU 144145, 10 (16.45–19.80 mm), both same locale as holotype. Columbus Co.: MCZ 62123, 93 (13.30–18.70 mm), ditch parallel to State Rt. 1928, W Juniper Creek, 7.7 km E Old Dock; MCZ 62130, 4 (18.90–22.35 mm), pond next to Juniper Creek at State Rt. 1928 bridge, 7.7 km E Old Dock; MCZ 62129, 7 (18.00–20.80 mm, 4 cleared and stained) and UF 44427, 8 (19.80–21.50 mm), both Big Creek at bridge on State Rt. 1947, N side Lake Waccamaw. SANTEE RIVER DRAINAGE: SOUTH CAROLINA: Kershaw Co.: USNM 200628, 18 (15.30–18.75 mm) and MCZ 59312, 8 (16.35–21.50 mm), both Big Pine Tree Creek at State Rt. 131 bridge, 4.8 km E Camden.

Nontype Material. WACCAMAW RIVER DRAINAGE: NORTH CAROLINA: Brunswick Co.: Juniper Cr. at type locality, MCZ 62131 (17 specimens), UNC 10483 (13), NCSM 12831 (13); ditch W Juniper Cr., NCSM 12832 (61), NCSM 12833 (61); Big Cr., UNCW 79-26 (5), UNCW 80-15 (8), UNCW 80-53 (4). SOUTH CAROLINA: Georgetown Co.: tributary of Jericho Cr., Samworth Game Management Area, approximately 11 km NE Georgetown, AU 20518 (8), GMBL-84-36 (6), GMBL-84-37 (2), GMBL-84-38 (20), GMBL-84-41 (8), GMBL-84-42 (7).

DIAGNOSIS. Series of narrow dark bars on trunk distinguishes *E. boehlkei* from all other *Elassoma,* except *zonatum* and *okatie*. Differs from *zonatum* by its mode of 13 vertical trunk bars (9 in *zonatum*), mode of 27 lateral scales (31–33 in *zonatum*), and mode of 28 vertebrae (29 in *zonatum*). Lacks dark shoulder blotch and dark postocular stripe of *zonatum*. *Elassoma boehlkei* is most similar to *okatie*. Differs from *okatie* by its narrower bars (in male a mean width of 0.57 mm vs. 1.11 mm in *okatie,* and in female a mean width of 0.56 mm vs. 1.03 mm). Bars of *boehlkei* approximately same width as light interbar space (male *boehlkei* with a mean dark to light bar width ratio of 1.20 vs. 3.14 in *okatie,* and female *boehlkei* with a mean bar width ratio of 1.22 vs. 2.61 in *okatie*). Bars in *boehlkei* more numerous (mode 13) than in *okatie* (mode 11). Male *boehlkei* compared to *okatie* with relatively deeper body and caudal peduncle; longer predorsal, prepelvic, preanal, and head lengths; shorter dorsal and anal fins; and shorter snout (Table 4). Meristic values, except the lateral scale count, are significant at 0.0001 level. Female of *boehlkei* compared to *okatie* with fewer dorsal fin spines and anal fin and pectoral fin rays; shorter prepelvic, dorsal fin, and snout lengths; deeper body and head; and longer caudal peduncle and pelvic fin (Tables 4, 5). Trunk bars on female *boehlkei* often faint. Top of *boehlkei* head lacks scales, whereas that of *evergladei* is scaled.

DESCRIPTION. Small *Elassoma,* with mean adult length of 19.3 mm in male (77 specimens) and 19.3 mm in female (31 specimens). Largest specimen (male) measured was 27.0 mm. Counts and body proportions in Tables 1–4.

Bars on trunk (10)11–15(16). Bars narrow, in male average 0.57 mm (range 0.2–1.0) in width, 1.20 times wider than light interbar space (ratio range 0.81–1.66); in female average 0.56 mm (range 0.4–0.9), 1.22 times wider than light interbar space (ratio range 0.89–1.54). Bars crowded anteriorly.

Lateral scales (24)25–29(30), not pored. Scales in transverse row mode 15 (range 14–16). Scale rows around caudal peduncle mode 18 (range 17–19). Scales cover trunk; few scales embedded on the opercles and cheeks. Top of head scaleless.

Dorsal fin spines III-V (mode IV); dorsal fin soft rays (8)9–11(12). Last two dorsal fin rays joined in 35.8% of specimens examined. Anal fin spines III (one specimen with IV); anal fin soft rays (4)5–7(8); last two rays separate in 79.1% of specimens (joined in 20.9%). Pectoral fin rays mode 14, often number 15. Caudal fin branched rays 11 (range 9–13). Pelvic fin I,5; long and pointed; reaches anal fin.

TABLE 1. Proportional measurements of adults of *Elassoma boehlkei* from the type series (ANSP 158481, 158482). Proportions expressed as thousandths of standard length except last four which are proportions of head length. Student's t-test was used to test the significance between means. Levels of probability (P) greater than 0.05 were considered not significant (n.s.).

	21 males (includes holotype)				5 females				
Measurement	Holotype	Range	$\overline{X}$	SD	Range	$\overline{X}$	SD	t value	P
Standard length, mm	22.10	17.20–24.60	21.00	1.61	17.00–21.30	19.07	1.88	2.3470	.0275
Body depth	319	302–335	321	8.94	302–329	316	11.50	1.2030	n.s.
Predorsal length	495	464–512	483	12.72	458–516	488	25.08	−0.6354	n.s.
Prepelvic length	391	370–413	393	9.81	375–408	389	13.06	0.8262	n.s.
Preanal length	597	574–609	591	9.07	613–667	640	24.31	−7.6602	.0001
Dorsal fin length	351	325–384	356	15.34	304–373	335	27.69	2.4031	.0243
Anal fin length	186	173–221	195	12.28	146–192	161	18.83	5.0457	.0001
Caudal peduncle length	262	230–278	256	11.94	236–250	245	5.54	2.0186	n.s.
Caudal peduncle depth	142	131–157	142	7.01	118–136	123	7.60	5.2846	.0001
Pectoral fin length	145	114–155	134	10.09	100–139	127	16.36	1.2452	n.s.
Pelvic fin length	256	223–300	258	20.67	206–223	215	6.40	4.4998	.0002
Head length	353	330–366	349	10.32	329–353	343	10.43	1.1884	n.s.
Head depth	487	466–597	531	37.06	500–557	533	24.93	−0.1132	n.s.
Snout length	231	194–289	237	20.79	186–226	211	15.65	2.6207	.0150
Eye diameter	256	236–294	262	14.25	254–268	262	6.43	−0.0245	n.s.
Upper jaw length	308	241–308	287	15.54	233–274	245	16.38	5.3476	.0001

TABLE 2. Frequency of fin elements of *Elassoma boehlkei, E. okatie*, and *E. zonatum*. An asterisk indicates the holotypes.

	Dorsal fin spines							
Species	3	4	5	6	No.	Mean	SD	SE
E. boehlkei								
Waccamaw R (upper)	17	143*	32		192	4.08	.50	.04
Waccamaw R (lower)	2	27	17		46	4.33	.56	.08
Santee R		18	8		26	4.31	.47	.09
E. okatie								
Edisto R		6	1		7	4.14	.38	.14
Savannah R	1	93	86	3	183	4.50	.54	.04
New R	1	35*	46	1	83	4.57	.54	.06
E. zonatum								
North Carolina		38	83	4	125	4.73	.51	.05
South Carolina		35	49	1	85	4.60	.52	.06

	Dorsal fin rays									
	7	8	9	10	11	12	No.	Mean	SD	SE
E. boehlkei										
Waccamaw R (upper)		11	68	75*	12		166	9.53	.73	.06
Waccamaw R (lower)			10	26	10		46	10.00	.67	.10
Santee R			5	8	12	1	26	10.35	.85	.17
E. okatie										
Edisto R				3	4		7	10.57	.53	.20
Savannah R		2	25	105	42	4	178	10.12	.71	.05
New R			13	49*	19		81	10.07	.63	.07
E. zonatum										
North Carolina	1	10	43	57	10	1	122	9.56	.82	.07
South Carolina		3	28	42	4	1	78	9.64	.70	.08

	Anal fin rays									
	3	4	5	6	7	8	No.	Mean	SD	SE
E. boehlkei										
Waccamaw R (upper)		8	53	85*	23	1	170	5.74	.77	.06
Waccamaw R (lower)			3	25	16	2	46	6.37	.68	.10
Santee R			7	15	4		26	5.88	.65	.13
E. okatie										
Edisto R			1	4	2		7	6.14	.69	.26
Savannah R		4	28	85	60	3	180	6.17	.79	.06
New R			5	30	44*	1	80	6.51	.64	.07
E. zonatum										
North Carolina	1	20	55	43	3		122	5.22	.78	.07
South Carolina		8	25	43	2		78	5.50	.72	.08

	Pectoral fin rays								
	13	14	15	16	17	No.	Mean	SD	SE
E. boehlkei									
Waccamaw R (upper)	7	29*	33	4	1	74	14.50	.80	.09
Waccamaw R (lower)	2	21	21	1		45	14.47	.62	.09
Santee R	5	18	3			26	13.92	.56	.11
E. okatie									
Edisto R		1	4	1		6	15.00	.63	.26
Savannah R		16	59	18		93	15.02	.61	.06
New R	1	12*	24	8		45	14.87	.73	.11
E. zonatum									
North Carolina	1	10	31	34	4	80	15.38	.82	.09
South Carolina		9	20	12	2	43	15.16	.81	.12

TABLE 3. Frequency of lateral scales, vertical trunk bars, and total vertebrae number of *Elassoma boehlkei*, *E. okatie*, and *E. zonatum*. An asterisk indicates the holotypes.

	Lateral scales																
Species	24	25	26	27	28	29	30	31	32	33	34	35	36	No.	Mean	SD	SE
E. boehlkei																	
Waccamaw R (upper)	1	5	16	19*	15	8	1							65	27.08	1.25	.16
Waccamaw R (lower)		2	5	15	9	3								34	27.18	1.00	.17
Santee R		1	5	9	10									25	27.12	.88	.18
E. okatie																	
Edisto R					5	1								6	28.17	.41	.17
Savannah R		5	12	30	23	16	6							92	27.55	1.26	.13
New R	3	10	22*	12	6	3	1							57	26.37	1.29	.17
E. zonatum																	
North Carolina							10	16	13	21	11	4	3	78	32.40	1.58	.18
South Carolina					1	3	12	9	9	4	3	1		42	31.21	1.55	.24

	Trunk bars													
	7	8	9	10	11	12	13	14	15	16	No.	Mean	SD	SE
E. boehlkei														
Waccamaw R (upper)				3	7	22	24*	12	5	1	74	12.73	1.24	.14
Waccamaw R (lower)					6	13	16	7	1		43	12.63	1.00	.15
Santee R						6	13	6	1		26	13.08	.80	.16
E. okatie														
Edisto R			1		3	1		1			6	11.33	1.63	.67
Savannah R		1	5	20	37	26	4				93	11.01	.99	.10
New R		3	12	29	11*	2					57	9.95	.87	.11
E. zonatum														
North Carolina		10	30	23	17	1					81	9.62	.99	.11
South Carolina	1	12	17	10	3						43	9.05	.95	.14

	Total vertebrae								
	27	28	29	30	31	No.	Mean	SD	SE
E. boehlkei									
Waccamaw R (upper)	8	101	45*	1		155	28.25	.55	.04
Waccamaw R (lower)		8				8	28		
Santee R		20	3			23	28.13	.34	.07
E. okatie									
Edisto R	—	—	—	—	—				
Savannah R	1	70	40	1		112	28.37	.52	.05
New R	7*	31	3			41	27.90	.49	.08
E. zonatum									
North Carolina		2	35	16	1	54	29.30	.57	.08
South Carolina		7	57	16		80	29.11	.53	.06

Precaudal vertebrae mode 11 (range 10–13); caudal vertebrae mode 17 (range 16–19); total vertebrae mode 28 (range 27–30). Insertion of first dorsal pterygiophore usually between neural spines V and VI.

Gill rakers on lower arch usually six small fleshy knobs, rarely five or seven. Branchiostegals five. Sensory pores on head common and conspicuous.

Elongate villiform teeth on both jaws, absent from palatines. Two tiny teeth on vomer. Premaxilla covered with teeth in several rows; number of rows increases medially. Almost all teeth pointed inward, except some enlarged teeth (ca. 12 total) in outer margin that jut out from bone. Mandibular teeth in several series near symphysis, one row laterally. Most teeth hook inward, but few (ca. 8 total) enlarged outer teeth on either side of symphysis jut outward. Pharyngeals not fused, covered with teeth similar to smaller ones on jaws, those on outer edge slightly enlarged.

COLORATION. *Life colors of reproductive male* (Fig. 1a). Trunk and all fins except pectoral black; trunk from pectoral fin insertion to caudal fin base with series of brilliant green-blue bars separated by apparent black bars. Trunk may be dark brown and brilliant bars green, green-yellow, gold-green, or blue-green; some black flecks typically present throughout bars. Last brilliant bar often off-white, brown-white, or brown, sometimes divided into upper and lower halves by black scales; brilliant bar anterior to previous often brown. Bars typically complete, but sometimes only lower half or third is fully colored; bar edges irregular.

On side of head a brilliant green-blue postorbital bar from just below eye level to mid-eye level, a green-blue brilliant suborbital spot or short bar, and weak similar-colored spot on antero-lower edge of eye. Few or many brilliant green-blue flecks on operculum and adjacent thorax. Brilliant bars, spots, and flecks may vary in color as in trunk bars.

Dorsum black or dark brown, posterior half often of alternating black and green-blue (meeting of lateral bars). Underside of mouth gray with black stipples, sometimes weakly mottled; underside of thorax mottled light and dark black; rest of venter of alternating black and green-blue (meeting of lateral bars).

Pectoral fin clear. All other fins usually black, darkest on distal edges and on rays. Dorsal fin with 3 to 4 white spots on rays on lower two-thirds to three-fourths of fin; spots lacking on spines. A row of distinct black dots on bases of all fin supports. Caudal fin with 2 or 3 white spots on por-

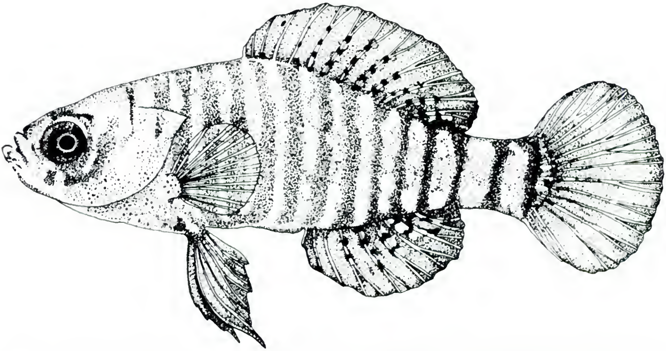


FIG. 1a. *Elassoma boehlkei*, breeding male, one of a series of 27 males, 16.0–21.5 mm SL ($\bar{x}$ = 19.0 mm), from the type locality, 22 March 1984. ANSP 159035.

TABLE 4. Proportional measurements of adult specimens of *Elassoma boehlkei* (43 males, 15 females) and *E. okatie* (23 males, 18 females). Proportions expressed as thousandths of standard length, except last four which are proportions of head length. Student's t-test was used to test the significance between means. Levels of probability (P) greater than 0.05 were considered not significant (n.s.).

	E. boehlkei			*E. okatie*				
Measurement	Range	$\overline{X}$	SD	Range	$\overline{X}$	SD	t value	P
Male								
Standard length, mm	15.25–24.60	19.26	2.04	16.50–28.70	21.18	3.04	−5.1657	.0001
Body depth	302–360	325	13.83	276–335	312	14.56	3.6647	.0007
Predorsal length	442–520	489	16.61	449–499	469	12.82	5.3590	.0001
Prepelvic length	370–425	397	10.17	377–415	390	8.17	2.9331	.0049
Preanal length	574–617	594	10.16	558–605	584	12.36	3.1435	.0032
Dorsal fin length	325–387	358	16.01	342–394	374	13.01	−4.2477	.0001
Anal fin length	168–223	201	14.02	185–234	210	13.88	−2.7241	.0091
Caudal peduncle length	201–278	244	16.77	210–258	238	10.85	1.8334	n.s.
Caudal peduncle depth	130–163	143	6.91	121–149	136	7.11	3.4634	.0012
Pectoral fin length	108–168	136	12.44	114–156	133	10.49	0.7715	n.s.
Pelvic fin length	222–320	263	21.54	237–307	271	17.72	−1.5119	n.s.
Head length	330–376	355	12.77	317–370	347	11.83	2.6510	.0108
Head depth	464–682	548	51.35	484–606	549	32.40	−0.0784	n.s.
Snout length	180–289	230	24.87	193–293	246	23.50	−2.5806	.0130
Eye diameter	236–305	265	16.22	232–293	257	15.86	1.7992	n.s.
Upper jaw length	241–343	285	18.71	227–318	276	26.30	1.5258	n.s.
Female								
Standard length, mm	16.20–22.50	19.29	1.78	16.20–26.85	20.98	3.17	−2.7272	.0085
Body depth	281–344	322	18.83	254–368	298	26.22	3.1535	.0036
Predorsal length	458–516	490	17.58	451–506	478	18.44	1.9108	n.s.
Prepelvic length	348–408	388	14.08	382–437	406	14.76	−3.5665	.0012
Preanal length	595–680	633	23.92	629–669	644	11.26	−1.6512	n.s.
Dorsal fin length	296–373	338	22.79	302–418	360	33.39	−2.3044	.0283
Anal fin length	146–192	171	15.59	143–230	178	24.51	−0.9958	n.s.
Caudal peduncle length	205–250	232	14.50	188–249	218	18.32	2.5268	.0168
Caudal peduncle depth	117–136	123	5.79	93–143	120	11.12	1.2923	n.s.
Pectoral fin length	99–160	124	18.83	103–143	126	9.22	−0.3736	n.s.
Pelvic fin length	187–272	219	25.00	167–243	200	23.96	2.2828	.0298
Head length	298–370	337	19.37	322–415	349	19.95	−1.7772	n.s.
Head depth	470–614	543	38.84	387–560	512	41.06	2.2370	.0327
Snout length	179–242	208	18.14	168–271	229	32.70	−2.3360	.0271
Eye diameter	248–298	273	13.83	234–319	268	21.70	0.8532	n.s.
Upper jaw length	233–313	259	22.53	212–295	244	22.03	1.9421	n.s.

tions of rays in proximal half of fin; spots absent from distal half of fin and from rays near upper and lower edges of tail. Anal fin with 3 or 4 white spots on each ray on proximal half to three-fourths of fin; spots absent from spines. Pelvic fin with approximately 5 white spots on proximal portion of last 4 rays; spots absent from first ray and spine. White spots form columns and rows on extended dorsal, caudal, and anal fins, less so on pelvic fin. Rays and interradial membranes of colored fins may be covered with many minute green-blue flecks.

Pupil black, surrounded by narrow light brown ring; rest of eye black.

Life colors of reproductive female (Fig. 1b). Trunk brown, with weak and complete light brown trunk bars separated by darker brown bars; bars present from pectoral fin insertion to base of caudal fin. Last bar

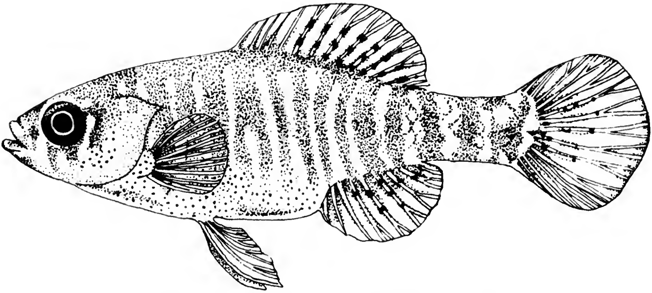


FIG. 1b. *Elassoma boehlkei*, breeding female, one of a series of six females, 16.5–19.5 mm SL ($\bar{x}$ = 17.8 mm), from the type locality, 22 March 1984. ANSP 159035.

often white-gray, often divided into upper and lower halves by brown scales. Edges of trunk scales suffused with melanophores, may give trunk a weak cross-hatched appearance. Green-blue postorbital bar from below eye level to mid-eye level, light colored suborbital bar or spot, and white-gray bar or spot at antero-lower corner of eye; green-blue color often white-gray; white-gray bars/spots each bordered posteriorad by dark brown bar. Brilliant green-blue flecks on lower operculum, on adjacent thorax, and sometimes on side of trunk. Dentary often darker brown than adjacent areas of jaw. Branchial area usually brown-pink (blood); posterior thorax usually brown-yellow (ova). Vertebral column and associated ventral major blood vessels often visible in posterior trunk.

Top of snout gray; area above eye black (from contained portion of eye). Dorsum posteriorad to middle of dorsal fin medium brown, remainder of dorsum to caudal fin alternating lighter and darker brown (from meeting of lateral bars).

Lower jaw posteriorad to isthmus gray, isthmus gray, ventral branchial area gray-pink (blood), posterior half of thorax gray-orange (ova), all black-stippled. Remainder of venter alternating dark and light brown (meeting of lateral bars).

Pectoral and pelvic fins clear. Dorsal fin with approximately 3 brown or black spots on each but anterior 2 or 3 fin supports, lowest row of spots adjacent to dorsum. Areas between dark spots white in contrast. Caudal fin with gray-black rays; rest of fin clear except for dark smudges on

TABLE 5. Selected meristic counts of adult females of *Elassoma boehlkei* and *E. okatie*. Student's t-test was used to test the significance between means.

	E. boehlkei (36 specimens)			*E. okatie* (42 specimens)				
Meristics	Range	$\bar{X}$	SD	Range	$\bar{X}$	SD	t value	P
Dorsal fin spines	3–5	4.0	0.51	4–6	4.7	0.57	−5.2729	.0001
Anal fin rays	4–7	5.8	0.72	4–8	6.2	0.93	−2.2223	.0298
Pectoral fin rays	13–17	14.2	0.65	13–16	14.8	0.76	−3.7187	.0004

rays in middle of fin. Anal fin with approximately 3 dark spots on most fin supports, but absent on anterior 2 or 3 fin supports. Areas on rays between dark spots appear white in contrast. Spots form columns and rows on spread dorsal and anal fins.

Pupil black, surrounded by yellow ring; rest of eye light brown.

Colors in alcohol of reproductive male. Brilliant trunk bars on freshly-preserved fish hyacinth-blue, later fade into light-colored bars. Trunk with alternating brown-black and light brown bars, last bar light brown; bars complete from pectoral fin insertion to caudal fin base. Some specimens with 1 weakly-defined light bar and 1 dark bar, and occasional specimens with 2 light bars and 2 dark bars in advance of pectoral insertion; bars incomplete, extend from top of operculum almost to top of dorsum. Scales of dark bars heavily suffused with melanophores, particularly on scale edges. Scales of light bars lacking, or with few, melanophores, except for black-pigmented scale edges. Top of head black, nape and dorsum to level of dorsal fin origin dark brown, remainder of dorsum of weakly-defined darker and lighter areas (tops of alternating dark and light trunk bars).

Lower jaw to anus uniform medium brown, with dark stippling. Branchiostegal membrane heavily black-stippled. Venter from anus to tail of alternating light and dark brown-black (meeting of lateral trunk bars).

Side of head and operculum brown with pronounced brown-black flecking. Prominent light brown postorbital bar from level of mouth to level of mid-eye, prominent light-brown suborbital bar from level of mouth almost to eye, and a weakly-defined light brown spot at antero-lower edge of eye and next to maxilla; light bars and spot bordered by strong black stippling.

Upper jaw brown-black, heavily black-stippled except for 2 light-brown patches posteriorad on each side. Lower jaw dark brown, heavily melanophore-stippled, except for light-brown patch on middle to middle-posterior of side of each dentary.

Dorsal fin smoky black, heavily black-stippled, particularly on anterior edge and posteriorad fourth of fin. Anterior ray with 1 indistinct white spot, last 3 or so rays with 2 prominent white spots, and all other rays with 3 to 4 conspicuous white spots; spots in mid-fin area, except posteriorad where are nearer fin base. Upper and lower edges of white spots accentuated by clusters of melanophores. Rays melanophore-stippled, but less so and lighter-colored than interradial areas. Indistinct dark smudge at bases of rays, next to dorsum.

Caudal fin interradial areas brown, evenly stippled with melanophores. Rays less stippled and not as dark. Eight to 10 indistinct light brown spots present on proximal two-thirds of most of tail rays; spots absent from ray bases, and from upper and lower 3 or 4 rays.

Anal fin smoky black, heavily black-stippled. Rays less stippled and not as dark. Two or 3 white spots on first 2 rays, 3 or 4 similar spots on other rays. Indistinct brown-white smudge on bases of rays and second and third spines.

Pelvic fin smoky black, heavily black-stippled; rays not as dark. Two or 3 white spots on proximal third to half of third, fourth, and fifth rays.

Pectoral fin mostly clear. Rays bordered by rows of small melanophores. Proximal third of fin with extensive black-stippling, particularly on margins.

Pupil opaque, rest of eye gray-black.

Colors in alcohol of reproductive female. Trunk with weak alternating medium brown and light brown bars, last bar light brown. Bars complete from anus to caudal fin base, weaker and incomplete (on dorsal half of side) from anus to pectoral fin. Scales of dark bars strongly suffused with melanophores. Light bar scales lacking, or with few, melanophores, except for heavily-pigmented scale edges. Top of head dark brown, nape to dorsal fin origin medium-brown, rest of dorsum of weak alternating medium and light brown (tops of trunk bars).

Lower jaw, isthmus, and breast to pectoral fin and pelvic fin insertions light brown, with scattered melanophores; stipples on breast larger than others. Branchiostegal membrane less black-stippled than in male. Venter from pelvic fin insertion to urogenital opening brown-yellow (contained ova), remainder of venter to tail of alternating light and medium brown (meeting of lateral bars).

Side of head and operculum brown, with flecking of melanophores, but less so than in male. Weak light-brown postorbital bar from level of mouth to level of mid-eye, weak light-brown suborbital bar from level of mouth almost to eye, and weak small light brown spot from antero-lower edge of eye to angle of mouth.

Upper jaw light brown, heavily stippled with melanophores; posterior end of jaw lighter in color, with only scattered stipples. Lower jaw dark brown, heavily black-stippled, except for distinct light-brown patch on middle to posterior end of each dentary.

Dorsal fin mostly clear. Three prominent brown-black spots on, but wider than, all rays but last; last ray with only 2 spots. Proximal row of spots next to dorsum, most distal row at two-thirds of length of ray from trunk. Interradial areas of distal third of fin clear. Branched portions of rays edged by fine melanophores. Spines and interspine membranes with fine black stipples, stipples forming 2 or 3 weak black clusters along length of posterior 2 or 3 spines. Basal portion of dorsal with prominent brown-black stipples. Dark spots on fin form symmetrical rows and columns on clear background.

Caudal fin mostly clear. All rays edged with fine black stipples. Some stipples present throughout interradial areas, particularly on proximal three-fourths of fin. Small clusters of melanophores along all rays, except approximately upper and lower 3 rays, these weak dark spots separating indistinct white spots. Light and dark spotting most conspicuous on middle 6 rays, from near tail base to first branch of rays.

Anal fin mostly clear. Three or 2 prominent brown-black spots of melanophores on each ray and extending onto adjacent interradial areas. Spots form rows, most proximal row almost by trunk and most distal some half to two-thirds length of ray from trunk. Scattered black stipples on ray edges, from level of most distal spots to ends of rays. Basal portion of fin with brown-black stipples.

Pelvic fin clear. Pectoral fin mostly clear, but edges of rays and branches to tips bordered with fine black stipples.

SEXUAL DIMORPHISM. Breeding male highly colorful, female drab. Color of non-reproductive male essentially that of female. Dorsal, anal, and pelvic fin of male longer than of female (Table 1). Preanal length shorter in male. Snout and upper jaw longer in male. Caudal peduncle deeper in male. No sexual difference in meristic counts noted.

DISTRIBUTION, ABUNDANCE, AND VARIATION. The Carolina pygmy sunfish is known from two areas in the Waccamaw River drainage, and one in the middle Santee River drainage (Fig. 2). One of the two Waccamaw River areas, the upper Waccamaw, contains two population centers, both in North Carolina. One of these is in Juniper Creek, which joins the Waccamaw downstream of Lake Waccamaw in Brunswick and Columbus counties, and the second is in a roadside ditch that drains into Big Creek, tributary to Lake Waccamaw, Columbus County. *Elassoma boehlkei* has been taken at six sites in the Juniper Creek system, where it

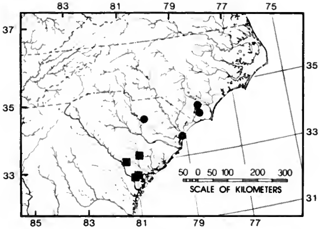


FIG. 2. North Carolina and South Carolina showing capture sites for *Elassoma boehlkei* (circles) and *Elassoma okatie* (squares).

is evidently widespread. The species is known from only one locality in the Big Creek system. The second Waccamaw River area is in the lower Waccamaw, and the population here occurs in old ricefield ditches off Jericho Creek in the Samworth Game Management Area, near Georgetown, Georgetown County, South Carolina. The Santee River population is restricted to a small pool adjacent to Big Pine Tree Creek, near Camden, Kershaw County, South Carolina.

No significant difference in meristics, morphometrics, or pigmentation was noted between populations.

The disjunct distribution of this species, which may represent a sampling artifact, is as yet unexplained. While additional sampling will likely fill distributional gaps, particularly in South Carolina, extensive sampling in the upper Waccamaw River drainage indicates that the species here is restricted to Juniper Creek and Big Creek (Shute et al. 1981).

Pronounced fluctuations in abundance of *E. boehlkei* may also explain an apparent disjunct population. In the late 1970s *E. boehlkei* was consistently outnumbered by *E. evergladei* in Juniper Creek (e.g. 16 *boehlkei* and 254 *evergladei* taken at type locality on 9 May 1977) but in the early 1980s the ratio was reversed (e.g. 30 *boehlkei* and 3 *evergladei* collected on 13 February 1984).

HABITAT AND ECOLOGY. The type locality at Juniper Creek is 30 m wide and to 1 m deep; current slow; water clear and brown (tannins); water level varies by about one m (annual, seasonal, and daily variations); substrate mud-sand, with much plant detritus. Luxuriant submerged and emergent aquatic vegetation includes a rush, *Juncus repens;* three-way sedge, *Dulichium arundinaceum;* golden club, *Orontium aquaticum;* and filamentous green algae (Zygnematales). Water temperatures ranged from 7.8°C to 27.8°C and pH values from 4.0 to 4.5 on 19 dates from November 1975 to April 1986. *Elassoma boehlkei* was collected near shore, to a depth of 0.5 m. The creek nearby is to 3 m deep.

Juniper Creek here is bordered by dense wooded swamp and shrub swamp of bald cypress, *Taxodium distichum;* red maple, *Acer rubrum;* sweet gum, *Liquidamber styraciflua;* black gum, *Nyssa sylvatica;* loblolly pine, *Pinus taeda;* pond pine, *Pinus serotina;* dahoon, *Ilex cassine* var. *myrtifolia;* titi, *Cyrilla racemiflora;* sweet pepperbush, *Clethra alnifolia;* button bush, *Cephalanthus occidentalis;* and others.

Elassoma boehlkei was the most common fish taken here. The 15 fish species collected with it were *Elassoma evergladei* and *Umbra pygmaea, Esox americanus, E. niger, Erimyzon oblongus, Chologaster cornuta, Aphredoderus sayanus, Fundulus lineolatus, Gambusia affinis, Enneacanthus chaetodon, E. gloriosus, E. obesus, Lepomis gulosus, Etheostoma fusiforme,* and *E. serriferum.*

The State Route 1928 roadside ditch site in the Juniper Creek system (see Paratypes for locality) is well-lighted, with scattered small *Acer rubrum, Ilex cassine,* and other low plants; water light brown; substrate of mud and of thick patches of submerged *Juncus repens,* Zygnematales, and other aquatics. The ditch, to 5 m wide and 0.9 m deep, is a series of shallow pools during drought. Water temperatures ranged from 5.0°C to 28.9°C and pH values from 4.0 to 6.9 on 16 dates from May 1977 to April 1986. Fishes were *E. evergladei,* many of the previous, and *Anguilla rostrata, Notemigonus crysoleucas, Ictalurus natalis, Acantharchus pomotis,* and *Centrarchus macropterus.*

A third site is a seasonal pond in lowland forest (see Paratypes) with brown water and a substrate of mud-sand and tree leaves; water depth was 0.6 m. The water temperature was 11.7°C in December 1982 and 7.8°C in November 1984, and the pH value in December was 4.5. Fishes were *Elassoma zonatum* and many of the previous.

Physicochemical and biological characteristics of other Juniper Creek localities and of the Big Creek site fall within the ranges of *E. boehlkei* habitat given above.

The Jericho Creek ricefield ditches site (see Nontype Material) is tidal freshwater, to 5 m wide and 1.0 m deep, with brown water and a mud substrate. The ditches are cut out of an alluvial delta with dense southern wild rice, *Zizaniopsis miliacea;* pickerelweed, *Pontederia cordata;* arrowhead, *Sagittaria* sp.; *Orontium aquaticum;* and others, and with abundant submerged watermilfoil, *Myriophyllum* sp., and Brazilian elodea, *Egeria densa.* Water temperature in April 1986 was 19.4°C, the pH value 6.9, and the dissolved oxygen content 4.5 ppm. Fishes were *Elassoma zonatum,* many of the previous, and *Lepisosteus osseus, Amia calva, Heterandria formosa, Lepomis gibbosus, L. punctatus,* and *Paralichthys lethostigma.*

The Santee River site (see Paratypes) is in lowland forest, in a 3 m by 6 m pool with a mud and detritus substrate and with tree branches and stems, and is intermittently connected to a fast-current, high-flow creek. Water-lily, *Nymphaea odorata,* was common. Water temperatures of 10.0°C and 15.6°C and pH values of 6.0 and 6.1 were recorded in a winter and a spring collection, respectively. Taken with *E. boehlkei* were *E. evergladei, E. zonatum,* and many of those listed for the type locality.

ETYMOLOGY. Named in honor of the late James E. Böhlke, Curator of Fishes, The Academy of Natural Sciences of Philadelphia, in recognition of his many contributions to ichthyology and of his long-standing interest in the genus *Elassoma.* The common name refers to the distribution of the species in the two Carolinas.

Elassoma okatie n. sp., Bluebarred pygmy sunfish, Figs. 3a and 3b, Tables 2–7

Holotype. ANSP 158483, 19.50 mm SL, adult male, New River Drainage, South Carolina, Jasper County, roadside ditch on U.S. Route 17, 0.8 km S Great Swamp Creek and 3.5 km S Switzerland, 4 Apr 1983, Arndt and Shedletsky.

Paratypes. NEW RIVER DRAINAGE: SOUTH CAROLINA: Jasper Co.: ANSP 158484, 71 specimens (15.35–20.50 mm), same collection data as holotype; TU 144146, 11 (20.60–26.45 mm), Causeway Swamp Creek, on U.S. Rt. 17, 8.8 km N Hardeeville. SAVANNAH RIVER DRAINAGE: SOUTH CAROLINA: Jasper Co.: ANSP 158485, 22 (21.35–27.15 mm), roadside ditch at second bridge on U.S. Rt. 321 and 2.7 km S Tillman; ANSP 150052, 34 (19.50–24.75 mm), MCZ 62125, 24 (18.85–23.80 mm), MCZ 62129, 4 (23.30–24.10 mm) (cleared and stained), USNM 279323, 32 (18.60–23.15 mm), UF 44428, 10 (19.20–23.15 mm), same locale; UMMZ 213589, 7 (20.30–26.75 mm), roadside ditch, E side U.S. Rt. 321, 4.8 km N Hardeeville.

Nontype Material. EDISTO RIVER DRAINAGE: SOUTH CAROLINA: Bamberg Co.: Edisto R., end State Rt. 434, approximately 7.5 km ESE Bamberg, GMBL-70-15 (1 specimen), NCSM 12834 (6). SAVANNAH RIVER DRAINAGE: SOUTH CAROLINA: Allendale Co.: Brier Cr., U.S. Rt. 301, 6.4 km WSW Allendale, NCSM 12835 (3). Jasper Co.: W side U.S. Rt. 321 ditch, ANSP 150053 (67). NEW RIVER DRAINAGE: SOUTH CAROLINA: Jasper Co.: Great Swamp Cr., U.S. Rt. 17, 16 km NE Hardeeville, CU 22059 (4).

DIAGNOSIS. Series of dark bars on trunk distinguishes *E. okatie* from all other *Elas-*

soma, except *zonatum* and *boehlkei*. Differs from *zonatum* by its lack of dark shoulder blotch, dark postocular stripe, mode of 11 vertical bars (9 in *zonatum*), mode of 27 lateral scales (31–33 in *zonatum*), and mode of 28 vertebrae (29 in *zonatum*). Most similar to *boehlkei, okatie* has wider bars (in male a mean of 1.11 mm vs 0.57 mm in *boehlkei*, in female a mean of 1.03 mm vs 0.56 mm in *boehlkei*) and which are approximately three times wider than light interbar space (in male a mean ratio of 3.14 vs. 1.20 in *boehlkei*, in female a mean of 2.61 vs 1.22 in *boehlkei*). Bars in *okatie* fewer (mode 11) than in *boehlkei* (mode 13). The male of *okatie* differs from *boehlkei* in several body proportions and all meristic counts except number of lateral scales (see *E. boehlkei* account and Tables 2–7).

DESCRIPTION. Moderate-sized *Elassoma* with mean length of 21.2 mm in adult male (108 specimens) and 21.0 mm in adult female (36 specimens). Largest specimen (male) measured was 28.70 mm. Counts and body proportions in Tables 2–7.

Bars on trunk (8)9–12(14). Bars wide, in male average 1.11 mm (range 0.6–1.8) in width, 3.14 times wider than interbar space (ratio range 2.07–4.23); in female, average 1.03 mm (range 0.7–1.6), 2.61 times wider than interbar space (ratio range 2.25–3.06). Bars wider anteriorly in both sexes.

Lateral scales (24)25–29(30), not pored. Scales in transverse row mode 16 (range 15–17). Scale rows around caudal peduncle mode 18 (range 15–19). Scales cover body; few scales embedded on the opercles and cheeks. Top of head scaleless.

Dorsal fin spines III-VI (mode IV); dorsal fin soft rays (8)9–11(12). Last two dorsal fin rays joined in 33.0% of specimens examined. Anal fin spines III (one specimen with IV); anal fin soft rays (4)5–7(8). Last two anal fin rays separate in 75.1% of specimens (joined in 24.9%). Pectoral fin rays mode 15. Caudal fin branched rays 12, occasionally 11. Pelvic fin I,5; long and pointed; reaches anal fin.

Precaudal vertebrae mode 11 (range 10–12); caudal vertebrae mode 17 (range 16–18); total vertebrae mode 28 (range 27–30). Insertion of first dorsal pterygiophore usually between dorsal fin spines V and VI.

Gill rakers on lower arch usually six small fleshy knobs, rarely five or seven. Branchiostegals five. Sensory pores on head common and conspicuous.

Elongate villiform teeth on both jaws, absent from palatines. One tiny tooth on vomer. Premaxilla covered with teeth in several rows, number of rows increases medially. All teeth pointed inward except for enlarged teeth (ca. 20) that jut out from bone on outer margin. Mandibular teeth in several series near symphysis, one row laterally. Most hook inward but few (ca. 6–7) enlarged outer teeth on either side of symphysis jut outward. Pharyngeals not fused, covered with teeth similar to smaller ones on jaws, those on outer edge slightly enlarged.

COLORATION. *Life colors of reproductive male* (Fig. 3a). Color almost identical to *boehlkei, okatie* distinguished by its greater size, and its fewer and wider black bars. Breeding male *okatie* typically black, while reproductive male *boehlkei* sometimes brown. However, this difference may be due to effects of habitat or sampling. Brilliant colors of adult male *okatie* typically blue-green, while *boehlkei* green-blue, but there is large overlap in color. Brilliant spot at anterior lower edge of eye conspicuous in *okatie* and relatively weak in *boehlkei*. Brilliant trunk bars of *okatie* always complete, while in *boehlkei* some or all bars sometimes incomplete toward dorsum.

Life colors of reproductive female (Fig. 3b). Color essentially as female *boehlkei*. Female *okatie* with more brilliant color

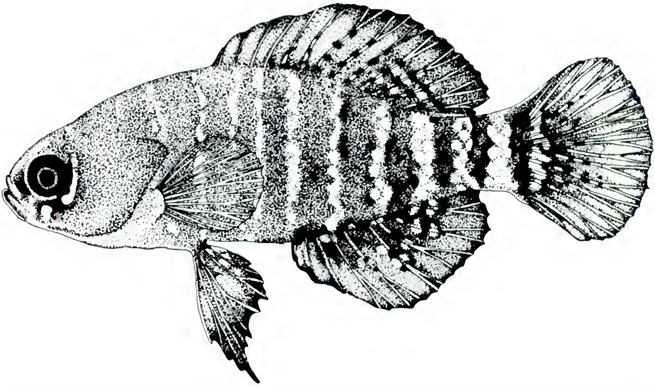


FIG. 3a. *Elassoma okatie*, breeding male, one of a series of four males, 25.0–26.0 mm SL ($\bar{x}$ = 25.7 mm), from roadside ditch on east side US 321, 13.5 km S Tillman, Jasper County, South Carolina, 25 March 1978. ANSP 159036.

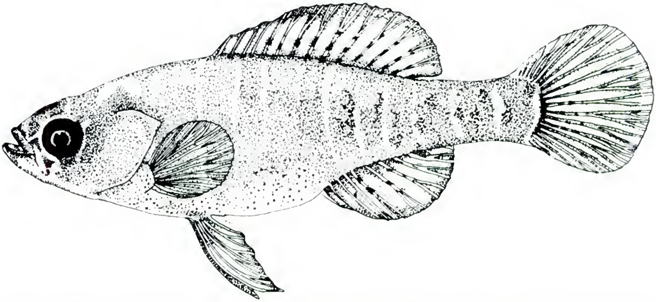


FIG. 3b. *Elassoma okatie*, breeding female, one of a series of six females, 20.7–26.1 mm SL ($\bar{x}$ = 22.7 mm), from west side US 17, at Causeway Swamp Creek bridge, 9.9 km N junction Interstate 95 and US 17, Jasper County, South Carolina, 19 March 1984. TU 144146.

than *boehlkei* on antero-lower eye spot and in flecks on thorax and mid-trunk. Brilliant color may appear blue, green, or yellow.

Reproductive females of *boehlkei* and *okatie* usually almost indistinguishable from those of *evergladei* and *zonatum*. Characteristic small trunk blotches of *evergladei* and the dark shoulder blotch and eye stripe of *zonatum* often not conspicuous until specimens are stressed or preserved.

Coloration of reproductive male in alcohol. The reproductive male *okatie* resembles *boehlkei* and usually differs only as follows: the lower part of the dentary below a light brown patch near the posterior end of the bone lacks stippling in *okatie* (stippling usually present in *boehlkei*); the last light brown trunk bar in *okatie* typically divided into upper and lower half by dark scales (bar usually complete in *boehlkei*); antero-lower eye spot more distinct in *okatie;* and postorbital bar usually longer in *okatie* (sometimes extends above eye).

Colors in alcohol of reproductive female. Similar to *boehlkei,* but *okatie* with less distinct dark spotting on dorsal and anal fins and with longer postorbital bar (extends from level below eye to almost or just above upper level of eye).

SEXUAL DIMORPHISM. Male highly colorful, female drab. Color of non-reproductive male very similar to that of female. Male with shorter preanal length, and longer anal fin (Table 6). Pelvic fin, pectoral fin, and dorsal fin of male longer, and caudal peduncle longer and deeper. Male with deeper head and longer snout and upper jaw. Trunk of female deeper, primarily due to developing ova. Sexual dimorphism in meristics noted only in dorsal fin spine and pectoral fin ray numbers, and in dark trunk bar number (Table 7).

DISTRIBUTION, ABUNDANCE, AND VARIATION. The bluebarred pygmy sunfish is known from three areas in the Edisto, New, and Savannah river drainages, all in southern South Carolina (Fig. 2). All known sites are pronouncedly man-impacted.

Most specimens were collected in roadside drainage ditches in Jasper County, New and Savannah river drainages (see Paratypes). *Elassoma okatie* here shows pronounced fluctuations in abundance as observed in *boehlkei*. The Savannah River population in Brier Creek is located between two highways. Only three specimens were collected here (one collection); *Elassoma zonatum* is common. The Edisto River specimens were taken near a boat ramp, where adjacent forest has been cleared. Only 11 *E. okatie* were collected here (7 collections); *E. zonatum* is common. At a site near Tillman, Jasper County, specimens were always readily obtained prior to July 1985 when none could be collected. It was moderately common again in March 1987.

Based on faded museum material at Cornell University, additional populations may occur in Savannah River tributaries in Georgia, but recent collecting has not found them.

No significant difference in meristics, morphometrics, or pigmentation was noted between populations.

HABITAT AND ECOLOGY. The type locality is a drainage ditch between a highway shoulder and a railroad bed. The ditch is probably man-created (to supply road fill). Ditch to 6 m wide, depth to 1 m; water brown and non-turbid; substrate mud-sand and plant detritus. Aquatic vegetation of dense broadleaf watermilfoil, *Myriophyllum heterophyllum;* hornwort, *Ceratophyllum demersum;* and others. A bladderwort, *Utricularia inflata,* was common nearby. Conspicuous ditch-edge vegetation was *Acer rubrum;* wax myrtle, *Myrica cerifera; Pinus taeda;* and *Liquidamber styraciflua*. Water temperatures ranged from 11.1°C to 32.0°C and pH

TABLE 6. Proportional measurements of adults of *Elassoma okatie* from the type series (ANSP 158483, 158484). Proportions expressed as thousandths of standard length except last four which are proportions of head length. Student's t-test was used to test the significance between means. Levels of probability (P) greater than 0.05 were considered not significant (n.s.).

	13 males (includes holotype)				9 females				
Measurement	Holotype	Range	$\overline{X}$	SD	Range	$\overline{X}$	SD	t value	P
Standard length, mm	20.00	16.50–26.70	19.00	1.98	16.20–26.85	18.56	3.90	0.3654	n.s.
Body depth	300	288–332	311	14.71	254–313	284	21.40	3.3194	.0055
Predorsal length	470	453–491	472	10.85	451–506	482	18.58	−1.4374	n.s.
Prepelvic length	382	382–415	392	8.94	382–437	402	17.09	−1.6163	n.s.
Preanal length	580	558–602	581	11.67	634–658	646	9.58	−14.1909	.0001
Dorsal fin length	388	355–388	373	10.27	360–418	388	22.56	−1.8481	n.s.
Anal fin length	220	193–234	215	11.17	171–230	197	19.93	2.4858	.0295
Caudal peduncle length	252	210–258	237	11.98	188–234	206	13.91	5.3861	.0001
Caudal peduncle depth	140	127–149	137	5.96	93–124	113	10.83	5.9910	.0001
Pectoral fin length	140	121–156	136	8.89	123–133	128	4.30	2.7144	.0141
Pelvic fin length	270	237–307	278	18.02	167–224	189	19.09	11.0729	.0001
Head length	340	340–370	351	8.76	342–415	358	23.08	−0.7788	n.s.
Head depth	588	500–606	550	31.85	387–531	490	46.00	3.4356	.0043
Snout length	250	229–286	250	18.60	168–246	205	29.18	4.0563	.0015
Eye diameter	265	235–286	261	13.56	234–319	276	25.60	−1.5798	n.s.
Upper jaw length	294	235–318	285	21.50	212–295	243	28.26	3.7121	.0023

TABLE 7. Selected meristic counts of adults of *Elassoma okatie* from the type locality. Student's t-test was used to test the significance between means.

	43 males			11 females				
Meristics	Range	$\overline{X}$	SD	Range	$\overline{X}$	SD	t value	P
Dorsal fin spines	4–5	4.6	0.49	4–6	5.0	0.45	−2.4079	.0196
Pectoral fin rays	13–16	14.9	0.71	13–16	14.3	1.01	2.2405	.0294
Dark trunk bars	8–12	9.9	0.83	9–12	10.4	0.93	−2.0113	.0485

values from 5.5 to 6.5 on 13 visits from June 1977 to April 1986.

The 17 fish species taken here were *Elassoma evergladei* and *Lepisosteus osseus*, *Esox americanus*, *E. niger*, *Erimyzon sucetta*, *Fundulus chrysotus*, *F. lineolatus*, *Gambusia affinis*, *Heterandria formosa*, *Labidesthes sicculus*, *Acantharchus pomotis*, *Centrarchus macropterus*, *Enneacanthus gloriosus*, *Lepomis gulosus*, *L. macrochirus*, *L. marginatus*, and *Etheostoma fusiforme*.

Elassoma okatie was also taken farther south in this ditch, to within 4.5 km N of Hardeeville. Conditions were similar to those at type locality. *Amia calva*, *Anguilla rostrata*, *Aphredoderus sayanus*, *Enneacanthus obesuss*, and many of the above were taken here with *E. okatie*. It is no doubt more widespread locally.

Elassoma okatie was also taken in drainage ditches on the west and east sides of Route 321 between Tillman and Hardeeville, Jasper County (see Paratypes). It is probably widespread in these ditches and nearby as appropriate habitat occurs throughout.

The Route 321 west ditch site is pond-like, approximately 80 m by 18 m, and between a highway shoulder and upland forest. The brown water is to 2 m deep over a mud-sand substrate with much detritus. Water temperatures ranged from 10.0°C to 31.1°C and pH values from 4.5 to 7.0 (usually 6.0–6.8) during 13 visits between March 1978 and March 1986. Abundant aquatic plants include duckweed, *Lemna minor;* pondweed, *Potamogeton* sp.; bladderwort, *Utricularia* sp.; rush, *Juncus* sp.; sedge, *Carex* sp.; and grasses, Poaceae. Conspicuous woody plant species include several of those found at the type locality and *Nyssa sylvatica;* willow oak, *Quercus phellos;* persimmon, *Diospyros virginiana; Ilex glabra; Cephalanthus occidentalis;* and palmetto, *Sabal minor*. Fishes were *E. zonatum* and most of those recorded for the type locality and nearby, and *Umbra pygmaea*, *Notemigonus crysoleucas*, *Notropis maculatus*, *Ictalurus nebulosus*, *Enneacanthus chaetodon*, *Lepomis auritus*, *L. gibbosus*, *L. punctatus*, and *Pomoxis nigromaculatus*.

The Route 321 east ditch site is also pond-like, 90 m by 30 m, and between a highway and successional forest. The brown water is to 1.5 m deep. The substrate is mud-sand and plant detritus. Water temperatures ranged from 10.0°C to 32.2°C and pH values from 5.8 to 6.5 on 10 visits between January 1978 and April 1986. In warm weather the pond is covered by *Nymphaea odorata* and water shield, *Brassenia shreberi; Juncus* sp. and bulrush, *Scirpus* sp., are common on shore. Conspicuous woody plants include those listed for the previous two sites. Fishes included *E. evergladei*, many of those noted for the previous two localities, and *Enneacanthus obesus* and *Micropterus salmoides*.

The Brier Creek site (see Nontype Material) is a brush-bordered creek backwater, to 40 cm deep with clear water, and with a mud-sand-detritus substrate. Unidentified aquatic vegetation was diverse, dense, and widespread. Water-side woody vegetation was young *Acer rubrum; Liquidamber styraciflua;* winged sumac, *Rhus coppalina;* alder, *Alnus* sp.; and tulip tree, *Liriodendron tulipifera*. On one visit in March 1985 the water temperature was 13.3°C and the pH value 6.5. Taken here was *E. zonatum* and 9 previously identified fish species.

The Edisto River site (see Nontype Material) is on a river backwater, in brown stained water to 2 m deep, with a substrate of mud-sand and detritus. Abundant in patches are alligatorweed, *Alternanthera philoxeroides; Potamogeton* sp.; spatterdock, *Nuphar lutea;* and duckweed, *Lemna* sp. Bordering forest contains conspicuous *Taxodium distichum;* water gum, *Nyssa aquatica; N. sylvatica; Liquidamber styraciflua;* water oak, *Quercus nigra;* river birch, *Betula nigra;* swamp willow, *Salix caroliniana; Sabal minor;* and cane, *Arundinaria gigantea*. Water temperatures were 12.8°C to 28.9°C and pH values 6.0 to 7.5 on 6 visits in the months March through August from 1983 to 1986. Taken here was *E. zonatum* and 15 of those previously recorded, and *Chologaster cornuta* and *Etheostoma serriferum*.

ETYMOLOGY. The species name is a euphonious derivative of the (local) Muskhogean Indian words for "oka," water, and "ateeh," coming from (Pickens 1963), and probably means aquatic. The name also honors the Okeetee Club, Switzerland, Jasper County, which has stimulated many biologists who have visited the area, and whose property borders most collection sites for *E. okatie*. The common name refers to the startlingly conspicuous brilliant blue bars on the breeding male.

COMPARATIVE MATERIAL EXAMINED. *Elassoma zonatum:* NORTH CAROLINA: CAPE FEAR DRAINAGE: Pender Co.: Angola Cr., MCZ 59308 (11 specimens). WACCAMAW RIVER DRAINAGE: Columbus Co., pond, Juniper Cr., MCZ 62140 (1); Beaverdam Swamp, MCZ 64295 (25). Brunswick Co.: Wet Ash Swamp, MCZ 62128 (23), UNC 10976 (9). SOUTH CAROLINA: PEE DEE RIVER DRAINAGE: Chesterfield Co.: Black Cr., NCSM 12836 (11). Sumter Co.: Pocotaligo R., ANSP 11030, (77). SANTEE RIVER DRAINAGE: Kershaw Co.: Big Pine Tree Cr., MCZ 59313 (8). EDISTO RIVER DRAINAGE: Bamberg Co.: Edisto R., ANSP 13573 (9). ASHEPOO RIVER DRAINAGE: Colleton Co.: trib., Ashepoo R., MCZ 59310 (67). COOSAWHATCHIE RIVER DRAINAGE: Hampton-Allendale cos.: Coosawhatchie R., MCZ 59304 (11). SAVANNAH RIVER DRAINAGE: Barnwell Co.: Savannah R., ANSP 95166 (22). GEORGIA: SAVANNAH RIVER DRAINAGE: Richmond Co.: Boggy Gut Cr., CU 17212 (1); Bulloch Co.: Lotts Cr., CU 18240 (2). Complete locality data available from the senior author.

STATUS AND CONSERVATION

No known population of either new species is now threatened. The relatively few known populations of both, however, and their occurrence mostly along roadsides, with attendant high risks from various types of potential habitat alteration or pollution, underscores their status as vulnerable. Both species should be given a large measure of protection by the appropriate state governments as well as by the Federal Government.

The barred pygmy sunfish, *Elassoma* sp., was listed as a species of concern in the U.S. Federal Register, Vol. 50, No. 181, p. 37958–37967, 18 September 1985. Both of the new species herein are under consideration for addition to the Federal Threatened Species List (R. Biggins pers. comm. 1985). No conclusion on their status has yet been reached. Wildlife agencies of both states and the U.S. Fish and Wildlife Service, however, are aware of the limited distributions of these fishes and consider this when commenting on proposed development plans.

KEY TO THE SPECIES OF *ELASSOMA*

1a. Scales on top of head; sides of trunk with light streaks or mottling; breeding male shiny black, female nondescript; from SE North Carolina through all of Florida (except the S tip) and into S Alabama. ....*Elassoma evergladei*
1b. Scales on top of head absent 2

2a. Distinct trunk bars absent; male shiny black with irregular blue trunk bars, female with irregular brown bars often broken into blotches; symphysis of lower jaw conspicuously depigmented; S Georgia and N half of Florida .... *Elassoma okefenokee*
2b. Dark trunk bars or blocks present, in females may be faint, or with blotches 3
3a. Postocular stripe present 4
3b. Postocular stripe absent 5
4a. One to three dark shoulder blotches (may be combined with trunk bars); 7–12 (usually 9) distinct dark and wide trunk bars; subocular bar usually prominent; 28–45 lateral scales; size large (up to 40 mm SL); Coastal Plain and lower Mississippi River Valley from North Carolina to Florida to S Illinois to E Texas and extreme SE Oklahoma .... *Elassoma zonatum*
4b. Shoulder blotch absent; subocular bar weakly developed; 5 or 6 wide block-like bars in male, 6–9 less well-defined bars (often blotches) in female; clear area in posterior portion of dorsal fin just anterior to a prominent black blotch in male; 28–30 lateral scales; restricted to one spring in north-central Alabama .... *Elassoma* n. sp.
5a. Dark trunk bars narrow (about 0.6 mm wide), about as wide as light (in life brilliant green-blue in male) interbar space; dark bars number 10–16 (usually 12–13); in upper (North Carolina) and lower (South Carolina) Waccamaw River Drainage, and middle Santee River system in Kershaw County, South Carolina ... . *Elassoma boehlkei*
5b. Dark trunk bars much wider (about 1.1 mm wide), about 3 times wider than light (in life brilliant blue-green in male) interbar space; dark trunk bars number 8–14 (usually 10–11); South Carolina .... *Elassoma okatie*

ACKNOWLEDGMENTS

We thank the following for their efforts in the deposition of types and comparative material: E. B. Böhlke (ANSP); K. E. Hartel (MCZ); W. M. Palmer (NCSM); R. D. Suttkus (TU); G. H. Burgess (UF); F. J. Schwartz (UNC); D. W. Nelson (UMMZ); and S. L. Jewett (USNM).

The following kindly allowed us to examine specimens in their care: W. G. Saul (ANSP); J. S. Ramsey (AU); R. Schoknecht (CU); W. D. Anderson and J. F. McKinney (GMBL); W. M. Palmer (NCSM); E. F. Menhinick (UNCC); D. G. Lindquist (UNCW); and R. P. Vari and S. L. Jewett (USNM).

Special thanks are given to the following colleagues and friends who have assisted in field work or given helpful advice: B. M. Burr, S. P. Epperly, D. F. Kapraun, D. G. Lindquist, G. W. Link, Jr., E. F. Menhinick, M. F. Mettee, Jr., J. F. Moyer, J. A. Pienta, D. N. Roark, C. C. Rohde, C. D. Rohde, S. W. Ross, J. Runningwolfe, J. D. Settle, S. Shedletsky, J. R. Shute, D. J. Sieren, R. D. Suttkus, and several Stockton State College students. We especially acknowledge the assistance of K. E. Hartel in providing space at MCZ for clearing and staining specimens and for facilitating the making of radiographs. The drawings are by E. S. Strack.

R. C. Cashner (UNO), K. E. Hartel (MCZ), R. E. Jenkins (RC), D. G. Lindquist (UNCW), and two anonymous reviewers made critical comments and provided helpful advice during manuscript preparation.

We thank the North Carolina Wildlife Resources Commission and the South Carolina Wildlife and Marine Resources Department for issuing the required scientific collecting permits.

LITERATURE CITED

AVISE, J. C., D. O. STRANEY, AND M. H. SMITH. 1977. Biochemical genetics of sunfish IV. Relationships of centrarchid genera. Copeia 1977(2): 250–258.

BÖHLKE, J. E. AND F. C. ROHDE. 1980. Accounts of *Elassoma evergladei* Jordan, *Elassoma okefenokee* Böhlke, and *Elassoma zonatum* Jordan. Pages 584–586, *in* D. S. Lee, C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer, Jr. Atlas of North American Freshwater Fishes. North Carolina State Museum Natural History, Raleigh. x + 867 pp.

BRANSON, B. A. AND G. A. MOORE. 1962. The lateralis components of the acoustico-lateralis system in the sunfish family Centrarchidae. Copeia 1962(1): 1–108.

HUBBS, C. L. AND K. F. LAGLER. 1958. Fishes of the

Great Lakes region. Cranbrook Institute Science, Bulletin No. 216, 213 pp.

Johnson, G. D. 1984. Percoidei: development and relationships. Pages 464–498 *in* H. G. Moser, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., W. J. Richards, and S. L. Richardson, eds. Ontogeny and systematics of fishes. Special Publication 1, American Society Ichthyologists Herpetologists, Lawrence.

Menhinick, E. F., T. M. Burton, and J. R. Bailey. 1974. An annotated checklist of the freshwater fishes of North Carolina. Journal Elisha Mitchell Scientific Society 90(1): 24–50.

Mettee, M. F., Jr. 1974. A study of the reproductive behavior, embryology, and larval development of the pygmy sunfishes of the genus *Elassoma*. Ph.D. Dissertation, University Alabama. 130 pp.

——— and J. S. Ramsey. 1986. Spring pygmy sunfish, *Elassoma* sp. Pages 4–5 *in* R. H. Mount, ed. Vertebrate Animals of Alabama in Need of Special Attention. Alabama Agricultural Experiment Station, Auburn University. 124 pp.

Pickens, A. L. 1963. Indian place-names in South Carolina. Pages 36–41 *in* Names in South Carolina. Published sporadically by the Dept. of English, University South Carolina, Vol. 10, Winter, 42 pp.

Roberts, F. L. 1964. A chromosome study of twenty species of Centrarchidae. Journal Morphology 115(3): 401–418.

Shute, J. R., P. W. Shute, and D. G. Lindquist. 1981. Fishes of the Waccamaw River drainage. Brimleyana No. 6: 1–24.

Proceedings of The Academy of Natural Sciences of Philadelphia 139: 87-158, 1987

Results of the Nepal Alpine Zone Research Project, Chironomidae (Diptera)

SELWYN S. ROBACK
Department of Entomology
The Academy of Natural Sciences of Philadelphia
19th and the Parkway, Philadelphia, PA 19103

WILLIAM P. COFFMAN
Pymatuning Laboratory of Ecology
Department of Biological Sciences
University of Pittsburgh, Pittsburgh, PA 15260

ABSTRACT.—The 97 species of Chironomidae collected from 69 stations in the Nepal Himalaya were primarily a Holarctic assemblage. The Orthocladiinae (50 species) was the dominant subfamily followed by the Chironominae (28 species). Within the Chironominae, the Tanytarsini (23 species) predominated. The genus *Micropsectra* dominated the Tanytarsini fauna. The Tanypodinae (10 species), Diamesinae (9 species) and the Chironomini (5 species) were more sparsely represented. No Podonominae were collected. The genus *Neopodonomus* Chaudhuri and Ghosh (1981), described from the central Himalaya is believed to belong to the Diamesinae genus *Boreoheptagyia* Brundin. Comparison is made with the Chironomidae collected on the Catherwood Bolivian-Peruvian Altiplano Expedition and the Northern European material reported by Thienemann (1941). [aquatic insects, Chironomidae, Diptera, fauna, Himalaya, Nepal]

This expedition was undertaken during May-June 1983 to study the distribution of high altitude flora and fauna in the Himalaya.

The Chironomidae were collected by Dr. Clyde Goulden, Dr. Richard Horwitz and Dr. Geoffrey Jacquez. Drs. Goulden and Horwitz are on the staff of the Academy of Natural Sciences of Philadelphia. Dr. Jacquez is on the staff of S.U.N.Y at Stony Brook, NY.

The treatments of the subfamilies Tanypodinae and Chironominae are by Roback; the Diamesinae and Orthocladiinae are by Coffman.

Unless otherwise indicated all Nepal specimens are in the collections of the Academy of Natural Sciences of Philadelphia. Specimens in Coffman's collection are marked COF. Larval descriptions, unless otherwise indicated, are of presumed fourth instar larvae. Earlier instars are indicated by (II or III).

PREVIOUS WORK

Papers on the Chironomidae of the Himalaya region, encompassing Northern India, Nepal, Kashmir, Afghanistan, Tibet and Bhutan are few and scattered. Kieffer, in a series of papers (1910, 1911a, b), described some species from Assam, Nepal and the western Himalaya. Edwards (1928) described two Diamesinae from Yunnan and Tibet. Thienemann (1936) described some chironomid larvae and pupae from Tibet. Tokunaga (1959) described *Himatendipes glacies* from Kashmir and in 1966 recorded it from Afghanistan. However, Sawedal and Willassen (1980) consider that *Himatendipes* is probably a synonym of *Micropsectra*. In 1968 Reiss described seven new Chironomidae species and one new genus (*Asclerina*) from Nepal. Lehman

(1969) described three *Rheocricotopus* from Nepal. Reiss (1971) described 18 Tanytarsini species from Nepal including the genera *Lauterbornia* now placed in *Micropsectra* (see Ashe 1983 for synonymy), *Tanytarsus*, *Micropsectra*, *Neozavrelia* and *Rheotanytarsus*. Five new *Micropsectra* species and three new *Tanytarsus* species were described. Saether and Willassen (1987) described the immatures of four new *Diamesa* species from Nepal, and Halvorsen and Saether (1987), in redefining and revising the genus *Tokunagaia*, described the pupa of a species (sp. A) from Darjeeling.

More recently, workers in India have published several papers on the eastern Himalaya fauna. Chaudhuri and Ghosh (1981) described what they considered to be a new podonomine genus (*Neopodonomus*) from Bhutan. The only Podonominae previously described from the Himalaya region were by Brundin (1966), who described two species of *Boreochlus* from the foothills of the eastern Himalaya in Northern Burma at 2000 m. In recent years Chaudhuri and colleagues have described numerous Orthocladiinae and Chironomini from eastern montane India. Chaudhuri et al. (1979) described 10 new species of *Limnophyes* and Chaudhuri and Ghosh (1980 and 1982) described some *Cricotopus* and *Orthocladius* from the eastern Himalaya. Chaudhuri et al. (1981), and Guha and Chaudhuri (1982) have described and recorded several *Polypedilum* species from Bhutan.

Abbreviations used in Tables 1-3 and/or descriptions are modified from Saether 1980b. The pupal thoracic chaetotaxy follows Coffman (1983).

PUPA

AL	anal lobes
AM	anal macroseta
Apo	apophyse
A.I-IX	abdominal segments
CT	cephalic tubercle
D$_{1-5}$	dorsal abdominal setae
Dcs	dorsocentral setae
FA	frontal apotome
FS	frontal setae
GS	genital sheaths
Hl	hooklets (recurved hooks)
L$_{1-5}$	lateral abdominal setae
Laps	lateral antepronotal setae
LS	flattened lateral abdominal filaments
Maps	median antepronotal setae
MD$_{1-3}$	dorsal muscle marks of abdomen
Mns	metanotal setae
Pas	prealar setae Pcs, precorneal setae
PLP	plastron plate of RO
PSA	pedes spurii A
PSB	pedes spurii B
RA	respiratory atrium
RO	respiratory organ
Sas	supra-alar setae (Dcs4)
V$_{1-4}$	ventral setae, abdomen
VT	vertex seta

LARVA

A$_{1-5}$	Antennal segments
ABl	accessory blade A$_1$
AP	anterior parapods
APe	antennal pedestal (Tanytarsini)
AR	antennal ratio
A.I-IX	abdominal segments
Bl	blade of A$_1$
Bl$_2$	blade of A$_2$ (Style)
CB	cardinal beard
CHL	chaetulae laterales
CHM	chaeta media
Cl	claws
CL	clypeus
CS, A$_1$, P$_1$, MD	campaniform sensillum
Dm	dorsomentum
DmT	dorsomental teeth
FA	frontal apotome
He	head
I$_t$	inner teeth of Li
L$_{1-4}$	lateral setae 1-4, abdomen
LaPc	lateral setae, procercus
Li	ligula
LL	labral lamella
LO	lauterborn organs
M	mentum
MD	mandible
Mo	mola
M$_t$	median tooth of Li

O	outer teeth of Li (=Li-L)
$P_{1,2}$	maxillary palpus
P_b	apical segments of maxillary palpus
Pc	procercus
PE	pecten epipharyngis
PG	pecten galearis
PH	pecten hypopharyngis
Pl	paraligula
PLO	pedicel of LO (Tanytarsini)
Pm	premandible
PmB	premandibular brush
PM	postmentum
PMa	pecten mandibularis
PO	postocciptal margin
PP	posterior parapods
S1, 2	labral setae
S3	clypeal seta
S.I	setae anteriores
S.II	setae posteriores
S.III	setae minuscula
S_{1-3}	lateroventral setae, MD
SA	supraanal setae
SAPe	spur of antennal pedestal
SBS	subbasal seta of PP
Si	seta interna, MD
Sl_2	labral sclerite 2
SP_2	sensory pegs A_2 (=LO)
SSd	seta subdentalis, MD
T.I.-III	thoracic segments
TA	anal tubules
TL	lateral tubules
TV	ventral tubules
Vm	ventromentum
VmP	ventromental plates

SPECIMENS EXAMINED

A	adult
La	larva
LEx	larval exuviae
P	pupa
PEx	pupal exuviae
PrP	prepupa

(II, III), instars II or III

In the descriptions and Tables L (length) and W (width) are used.

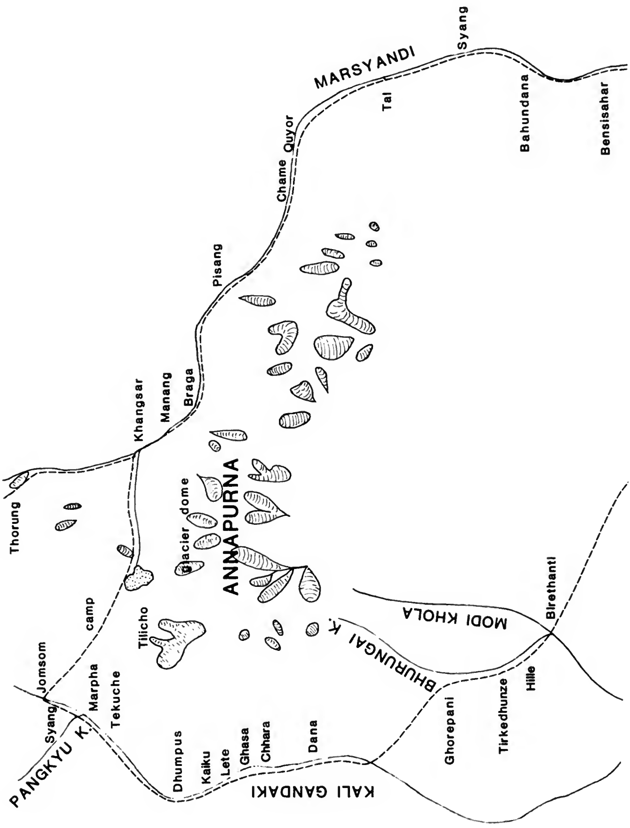
AREA COLLECTED

The area of the Nepal Himalaya from which collections were taken essentially encircles the Annapurna Massif and includes portions of the drainage basins of the upper reaches of the Kali Gandaki and Marsyandi (Marshyangdi) rivers. This area, shown in Map 1 is about165 km NW of Katmandu. Some collections were made from the Bhurungai Khola a major tributary of the Kali Gandaki and some of its feeder streams.

The two largest rivers collected are the Kali Gandaki and the Marsyandi. Both are glacial melt water streams and are blue-green to cloudy brown in color. The flow, especially in the upper reaches, varies with the heat of the day—lowest and more clear at night and early morning and higher and more brown during the warmest part of the day. This is also true of the melt water tributaries of these rivers. The spring fed rivers and streams, particularly the Bhurungai Khola and some of its tributaries were clear with more moss and algae on the bedrocks and boulders.

Above Ghasa, the Kali Gandaki flows through a wide valley in one to many channels—when collected in the dry season it was about 40-50 feet wide and one foot or less deep. In the rainy season it is about one quarter mile wide and very murky. Below Ghasa it cuts vertically more rapidly and flows through a more narrow valley. Here the bottom rubble consists of larger rocks and the river is 20-30 ft wide and 2-3 ft deep. The Marsyandi, in the area collected, was always narrower, 25 ft wide and 2-3 ft deep. As noted above, it is a melt water stream—blue-green and lower in the morning and more brown and higher later in the day.

Those tributaries which were spring fed with clear water were richest in Chironomidae. Of the 15 stations below 2000 m alt., NP14 and 18 with 14 and 12 species of Chironomidae, respectively, were the richest. Both were steep and clear with large rocks and boulders. NP18 consisted of a series of cascades. Of the 26 stations between 2000-3000 m alt., NP26 with 28 species of Chironomidae and NP38 with 23 species were the richest. NP38 was clear, rapid, and flowed through overhanging vegetation. The rubble was large and moss-covered. The three small streams comprising NP26 were clear, narrow, shallow, and completely exposed to the sun. The bottom was of rounded rocks and was filled with wood chips from an upstream sawmill. The



MAP 1. Area of Nepal from which collections were made; dashed line indicates expedition route.

organic loading here was apparently high. These streams entered the tributary represented by NP38 below that station. The description of NP 38 would fit the Bhurungai Khola in the area collected. Between 3000-4000 m, 14 stations were collected. Most had only 1-2 species of Chironomidae. Only NP134 (4 species) and NP83 and 89 (5 species each) had more species. Between 4000-5000m, 12 streams were collected. Of those only NP 90 (8 species) and NP 98 (7 species) had more than 1-2 species of Chironomidae. Both those collection areas were close to the apices of glaciers and were about 1 m wide and 7-10 cm deep. Above 5000 m only two small streams were collected and these had only 1 species (NP122) or 2 species (NP124) of Chironomidae. The overall geology of the Himalaya is still under study. Two articles encompassing the latest developments in our knowledge of the origin and structure of the Himalaya are by Molnar (1986) and Tapponier (1986).

Collection Locations

The following list gives the bodies of water collected in which Chironomidae were found. The locality, date, altitude and collector are given for each station. Overall over 150 localities were collected, but only the 69 stations from which Chironomidae were collected are listed here. The spelling of locality names is a problem, as no two maps have identical transliterations of the Nepalese names. The names used are primarily from the field notes of the collectors. Map 1 shows areas collected with the names of the principal towns.

NP4. Bhurungai Khola, Birethanti, 6-V-83, coll. Goulden, alt. 1046 m.
NP5. Bhurungai Khola, Birethanti, flat area, 7-V-83, coll. Goulden, alt. 1046 m.
NP7. Bhurungai Khola, Birethanti, 7-V-83, coll. Goulden, alt. 1530 m.
NP8. Bhurungai Khola, waterfall above Tirkedhunze, 7-V-83, coll. Goulden, alt 1530 m.
NP9. Kali Gandaki, Below Dana, 31-V-83, coll. Goulden, alt. 1360 m.
NP12. Tributary of Kali Gandaki with waterfall, N. of Dana 10- V-83, coll. Goulden, alt. 1462 m.
NP14. Tributary of Kali Gandaki, below waterfall, Chhara, 10- V-83, coll. Goulden, alt. 1548 m.
NP16. Tributary of Kali Gandaki, waterfall, Chhara, 31-V-83, coll. Goulden, alt. 1610 m.
NP17. Left bank Musi Khola, Trib. Marsyandi, Bahundana, 14-VI- 83, coll. Horwitz, alt. 1660 m.
NP18. Tributary of Kali Gandaki, below waterfall, Ghasa, 10-V- 83, coll. Goulden, alt. 2000 m.
NP19. Tributary of Marsyandi, above Tal, 12-VI-83, coll. Horwitz, alt. 2000 m.
NP21. Left bank tributary of Marsyandi, west end of Tal, 12-VI- 83, coll. Horwitz, alt. 2000 m.
NP22. Right bank tributary of Marsyandi, west end of Tal, 12-VI- 83, coll. Horwitz, alt. 2000 m.
NP23. Tributary of Kali Gandaki, Ghasa, 11-V-83, coll. Goulden, alt. 2135 m.
NP24. Tributary of Kali Gandaki, nr. Kaiku, 11-V-83, coll. Goulden, alt. 2135 m.
NP25. Tributary of Kali Gandaki, bedrock, before Kaiku, 30-V-83, coll. Goulden, alt. 2180 m.
NP26. Three small streams, tributaries of Bhurungai Khola, Nyathanti, 8-V-83, coll. Goulden, alt. 2250 m.
NP28. Tributary of Marsyandi, Quyor 11-VI-83, coll. Jacquez, alt. 2250 m.
NP32. Bedrock stream,tributary of Bhurungai Khola, Ghorepani, 2- VI-83, coll. Goulden, alt. 2390 m.
NP33. Bhurungai Khola, Hille, 2-VI-83, coll. Goulden, alt. 2390 m.
NP34. Bhurungai Khola below waterfall, Hille 2-VI-83, coll. Goulden, alt. 2390 m.
NP35. Bhurungai Khola, Birethanti, 2-VI-83, coll. Goulden, alt. 2390 m. NP37. Tributary of Kali Gandaki, Kalo Pani, 11-V-83, coll. Goulden, alt. 2480 m.
NP38. Mountain stream, tributary of Bhurungai Khola, Ghorepani, 8-V-83, coll. Goulden, alt. 2520 m.
NP39. Mountain stream, tributary of Bhurungai Khola, Ghorepani, 8-V-83, coll. Goulden, alt. 2520 m.
NP40. Kali Gandaki, Above Dhumpus, 11-V-83, coll. Goulden, alt. 2520 m.
NP41. Tributary of Marsyandi, nr. Quyor, 11-VI-83, coll. Jacquez, alt. 2520 m.

NP41. Tributary of Marsyandi, nr. Quyor, 11-VI-83, coll. Jacquez, alt. 2520 m.
NP42. Marsyandi, nr. Quyor, 11-VI-83, coll. Jacquez, alt. 2520 m.
NP43. Tributary of Kali Gandaki, nr. Tekuche, 11-V-83, coll. Goulden, alt. 2520 m.
NP44. Kali Gandaki, between Tekuche and Lete, 30-V-83, coll. Goulden, alt. 2660 m.
NP47. Tributary of Marsyandi, E end Chame, 10-VI-83, coll. Goulden, alt. 2660 m.
NP50. Tributary of Kali Gandaki, Syang, 12-V-83, coll. Goulden, alt. 2710 m.
NP51. Tributary of Kali Gandaki, Marpha, 11-V-83, coll. Goulden, alt. 2675 m.
NP54. Small pool of Kali Gandaki, North of Tekuche, 30-V-83, coll. Goulden, alt. 2600 m.
NP55. Reservoir nr. Langpoghyun Khola, across from Jomosom, 29-V- 83, coll. Goulden, alt. 2830 m.
NP56. Langpoghyun Khola, Jomosom, 29-V-83, coll. Goulden, alt. 2830 m.
NP69. Small Tributary of Marsyandi, nr. Manang, 8-VI-83, coll. Jacquez, alt. 3392 m.
NP71. Pond above right bank of Marsyandi, Below Pisang, 9-VI-83 coll. Horwitz, alt. 3400 m.
NP72. Tributary of Marsyandi, Braga, 7-VI-83, coll. Jacquez, alt. 3456 m.
NP73. Marsyandi, Braga, 6-VI-83, coll. Jacquez, alt. 3455 m.
NP75. Marsyandi, Manang, 5-VI-83, coll. Jacquez, alt. 3475 m.
NP76. Tributary of Marsyandi, Manang, 5-VI-83, coll. Jacquez, alt. 3495 m.
NP77. Lake, opposite Manang, 5-VI-83, coll. Jacquez, alt. 3500 m.
NP78. Small stream, Manang, 5-VI-83, coll. Jacquez, alt. 3500 m.
NP83. Tributary of Marsyandi, Khangsar, 24-V-83, coll. Goulden, alt. 3770 m.
NP85. Tributary of Langpoghyun Khola, Camp, 13-VI-83, coll. Goulden, alt. 3900 m.
NP89. Tributary of Langpoghyun Khola, Camp, 14-V-83, coll. Goulden, alt. 3995 m.
NP90. Glacial metal stream, Glacier dome Annapurna, 23-V-83, coll. Goulden, alt. 4025 m..
NP91. Springfed tributary of Marsyandi, Khangsar, 2-VI-83, coll. Horwitz, alt. 4050 m.
NP93. Glacial melt stream, Lake Tilicho, 29-V-83, coll. Goulden, alt. 4090 m.
NP98. Stream off moraine, Glacier dome, Anapurna 23-V-83, coll. Goulden, alt. 4100 m.
NP100. Small spring, Manang, 23-V-83, coll. Goulden, alt. 4155 m.
NP102. Small stream, below Thorung pass, Manang Valley, 4-V-83, coll. Jacquez, alt. 4240 m.
NP103. Valley stream of Marsyandi, Manang, 23-V-83, coll. Goulden, alt. 4250 m.
NP114. Tributary of Marsyandi, nr. Khangsar, 4-VI-83, coll. Horwitz, alt. 4630 m.
NP119. Marsyandi, above Khangsar, 4-VI-83, coll. Horwitz, alt. 4760 m.
NP120. Stream, nr. Tilicho, 29-V-83, coll. Goulden, alt. 4975 m.
NP121. Small tributary stream, Jomosom slide, Tilicho, 29-V-83, coll. Goulden, alt. 4985 m.
NP122. Tributary of Marsyandi, between Muktinath and Manang, 3- VI-83, coll. Horwitz, alt. 5860 m.
NP124. Glacial tarn, Thorung pass, 3-VI-83, coll. Jacquez, alt. 5860 m.
NP126. Tributary of Marsyandi, W. of Bensisahar, 14-VI-83, coll. Horwitz, alt. 850 m.
NP127. Sedge marsh, above Braga, 9-VI-83, coll. Horwitz, alt. 3500 m.
NP134. Tributary of Marsyandi, nr. Braga, 9-VI-83, coll. Horwitz, alt. 3500 m.
NP136. Large bedrock stream, Ghasa, 11-V-83, coll. Goulden, alt. 2135 m.
NP139. Springfed Tributary of Marsyandi, Tilicho, 23-V-83, coll. Goulden, alt. 4100 m.
NP144. Small stream, near Syang below Tal, 13-VI-83, coll. Jacquez, alt. 2300 m.
NP150. Tributary of Marsyandi, below Chame, 11-VI-83, coll. Jacquez, alt. 2470 m.
NP151. Left bank Tributary of Marsyandi, above Syang (ex. catfish guts), 13-VI-83, coll. Horwitz, alt. 1200 m.

Family CHIRONOMIDAE

Subfamily PODONOMINAE

No podonomines were found by this expedition. The only "podonomine" described from the central Himalayas is *Neopodonomus similis* Chaudhuri and Ghosh (1981). A review of the description of that species indicates that it is probably not a podonomine but rather falls in or close to *Boreoheptagyia* Brundin. The short costa, not to wing tip, does not fit the Podonominae. $R_{2,3}$ is very weak in *Boreoheptagyia* and may have been overlooked. The antennal structure of *N. similis* with flagellomeres 1-3 short, 4-12 slender with one whorl each and flagellomere 14 clubbed and subequal to 11+12 fits *Boreoheptagyia*. *Neopodonomus* has the following characters in common with *Boreoheptagyia*.:

(1) antennal structure; (2) costa not to wing tip. 3) wing with dense microtrichiae; (4) LR about 0.50; (5) tibiae with base and apex dark; (6) m-cu basal of fCu; (7) fCu at level of base of r-m; 8) biserial acrostichals, divergent around prescutellar area; (9) female with three spermathecae; (10) general male genitalic structure.

It differs in that the fourth tarsal segment is 0.66 the length of the fifth rather than 0.50.

Saether describes the female genitalia of *Boreoheptagyia* with gonapophysis VIII tongue -shaped, elongate as in *Neopodonomus*, and showed gonocoxite IX with setae on each side. This latter appears to be the structure which Chaudhuri and Ghosh call segment X. The differences are in the shape of the notum, more swollen in *Neopodonomus*, and the indistinct labia. Saether (1976b) describes the labia of *Boreoheptagyia* as being very large. A single larva of Boreoheptagyia was found at Station NP75, alt. 3475 m.

Subfamily TANYPODINAE

The Nepalese tanypodine fauna as represented by the 1983 collections is generically diverse but otherwise sparse. Nine genera are represented, but most by only one specimen. The generic composition is essentially Holarctic with all the genera found being represented in both the Palaearctic and Nearctic Regions. At the generic level, little can be said regarding any Ethiopian elements. Of all the genera, only *Conchapelopia* and *Thienemannimyia* were found below 2000 m. *Trissopelopia*, *Arctopelopia*, and genus nr. *Zavrelimyia* were found above 4000 m. The latter found at 5860 m represents the highest record for a tanypodine.

Tribe MACROPELOPIINI

Macropelopia (Apsectrotanypus) sp.

The single larva found is a typical member of the subgenus *Apsectrotanypus*. It differs little from the larva associated with *M. (A) johnsoni* (Coq.) (Roback 1978). The CS, P_1 is slightly more basad (Fig. 3) in the Nepalese specimen.

Larva. Head pale brown; A_1 241 μ; CS, A_1 0.75 from base; AR 6.34; A_2 (Fig. 4) 21 μ; L/W 3.0; A_3 3 μ; A_4 5 μ; Bl 32 μ; ABl 25 μ; Bl_2 13 μ; SP_2 5 μ; Bl/A_{2-4} 0.84; ABl/Bl 0.78; MD 222 μ; S_1 simple; $S_{2,3}$ appear multibranched; A_1/MD 1.09; P1 (Fig. 3) 76 μ; L/W 3.80; CS, P_1 (Fig. 3) 0.31 from base; A_1/P_1 3.17; P_b two segmented; Li (Fig. 1) 130 μ; I_t/O 0.82; M_t/O 0.74; Pl unevenly bifid; PH with about 17 even teeth; M as in Fig 2; with six DmT; Pc 222m; L/W 3.96; with 13 pale apical setae; TA concial, 185m; PP with 15 pale brown teeth; shape typical for subgenus.

SPECIMEN EXAMINED. NP69: lLa, alt. 3392 m.

Tribe PROCLADIINI

Procladius sp.

The single larva found is a typical *Procladius* (*Holotanypus*) species and would fall in either the *P. freemani* or *sublettei* group (Roback 1980).

Larva. Head pale brown; A_1 137 μ; CS, A_1 0.76 from base; AR 5.07; A_2 16 (Fig. 6); A_3 3 μ; A_4 4 μ; Bl (Fig. 6) 25 μ; ABl; 23 μ; Bl_2 8 μ; SP_2 5 μ; Bl/A_{2-4} 0.93; ABl/Bl 0.92; MD 144 μ; A_1/MD 0.95; P_1 (Fig. 7) 44 μ; L/W 2.75; CS, P_1 3.11; P_b two-segmented; Li (Fig. 5) 95 , apex black; I_t/0 0.89; M_t/0 0.85; PL (Fig. 5) 47 μ; with 1-2 inner teeth and 4-5 outer teeth; PH with 14 small teeth; M typical for genus; seven DmT; Pc 174 μ; L/W 3.11; 16 pale apical setae; TA conical, 241m; PP with 13-14 pale brown claws.

SPECIMEN EXAMINED. NP55: 1La, alt. 2830 m.

TABLE 1. Measurements (μ), ratios and mean of both for larvae of *Trissopelopia* and *Thienemannimyia* group: Range of altitude is given: A= absent; BR-Medium brown: DBR-dark brown; P=pale; - no data; + present; r=range of measurements. Numbers in [] after generic names = n for means, unless otherwise indicated.

	Trissopelopia [2]		Conchapelopia	Thienemannimyia [2]		Arctopelopia [2]	
	r	mean		r	mean	r	mean
A_1-L	377-381	379	-	281-285	283	303-330	316.5
CS, A_1	0.61-0.64	0.625	-	0.65-0.66	0.665	0.65-0.68	0.665
Spur A_1	A		-	+		+	
A_2-L	-	-	-	47-50	48.5	66	66.0 [1]
A_{24}-L	-	-	-	66-70	68	85	85.0 [1]
AR	-	-	-	4.01-4.32	41.65	3.5	3.56 [1]
F -L	72-73	72.7 [3]	67	53-53	53	58-67	62.5
CS,P_1	0.41-0.42	0.417 [3]	0.76	0.69-0.69	0.69	0.70-0.72	0.71
Pb segs.		2		3	2	2	
(0) Li-L	96-96	96	91	74-74	74	88-89	88.5
Mt/O	0.92-0.94	0.93	0.94	0.90-0.90	0.9	0.90-0.92	0.91
It/O	0.96-0.98	0.97	0.98	0.95-0.95	0.95	0.94-0.96	0.95
MD-L	163-170	166.7	185	133-137	135	85-89	87
MD S_2-S_3/S_3-CS	0.89-0.89	0.89	0.47	0.78-0.80	0.79	0.90-1.11	0.95
Ph Teeth	22-24	23.0 [3]	16	13-15	14	20-23	21.5
Pc-L	126-133	129.6 [3]	133	122-133	127.5	155-178	166.5
A_1/P_1	5.16-5.22	5.19	-	5.3-5.38	5.34	5.22-5.58	5.4
A_1/MD	2.22-2.34	2.28	-	2.05-2.14	2.095	1.91-2.24	2.075
Caud. He-CO		BR-DBR	P	DBR		BR	
Altitude (m)	2250-4100		1046-2390	1548		4025	

Tribe PENTANEURINI

THIENEMANNIMYIA GROUP

Members of this generic group were rather scarce and unfortunately many of the specimens found were in poor condition (see Table 1). Except for *Arctopelopia* ? sp. (4025-4155 m) most of the larvae were found below 2390 m. *Conchapelopia* lacks the spur-like projection found at the apex of A_1 in *Thienemannimyia* sp. and *Arctopelopia* ? sp. (Figs. 18, 19).

Conchapelopia sp.

Only a single poor fourth instar larva of this genus was found. The small inner MD tooth, the three-segmented P_b (Fig. 16), the simple SBS seta of the PP, and the position of S_3 of the MD (Fig.13) characterize this genus.

Larva. Apical antennal segments missing; essential characters and measurements given in Figs. 9, 13, 16 and Table 1.

SPECIMENS EXAMINED. NP4: 1La (?II), alt. 1046 m; NP5: 1La (?II), alt. 1046 m; NP18: 1La (?), alt. 2000 m; NP21: 1La (?III), alt. 2000 m; NP35: 1La (?III), alt. 2390 m.

Thienemannimyia sp.

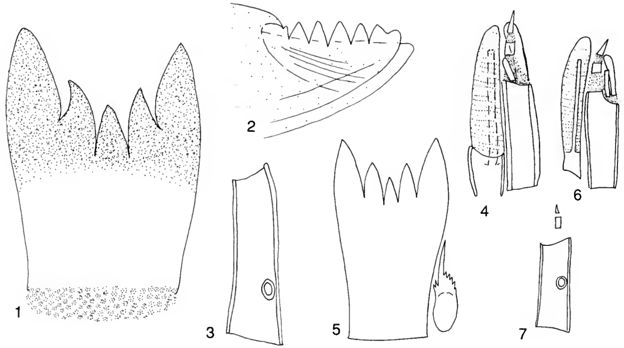
This genus, close to *Conchapelopia* has a two segmented Pb (Fig. 15) A1/MD>1.8 and dark caudal head margin.

Larva. Essential characters and measurements given in Figs. 8, 12, 15, 18 and Table 1.

SPECIMENS EXAMINED. NP14: 3La, alt. 1548 m.

Arctopelopia ? sp.

The placement of the two larvae in this genus is strictly tentative. Very few larvae of this genus have been associated and we have little idea as to



FIGS. 1-7. 1-4, *Apsectrotanypus* sp. larva: 1, Li; 2, DmT; 3, P1; 4, apex of antenna; 5-7, *Procladius* sp. 1. larva: 5, Li and Pl; 6, apex of antenna; 7, P_1 and P_b.

the extent of variation or whether the characters used to separate this genus in the larval stage will hold up when more larvae are associated. The large Li (Fig. 10), the high number of teeth on the PH (Fig. 10) and the distinct large spur apically on A_1 (Fig. 19) are used to place the two larvae here.

Larva. Essential characters and measurements given in Fig. 10, 11, 14, 17, 19 and Table 1.

SPECIMENS EXAMINED. NP90: 1la, alt. 4025 m;NP100:1La, alt. 4155 m

Trissopelopia sp.

This genus, whose Li (Fig. 20) resembles that of *Conchapelopia* is distinguished by the elongate P_1 with CS, P_1 (Fig. 23) just below the middle, the larger inner MD teeth (Fig. 24) and the flanged claws (Fig. 21) of the PP.

Larva. Apical antennal segments missing, essential characters and measurements in Figs. 20-24 and Table 1.

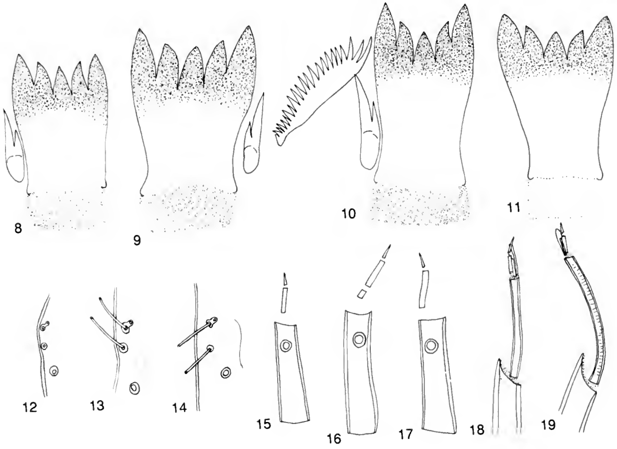
SPECIMENS EXAMINED. NP98: 1La, alt. 4100 m;NP26: 3La, alt. 2250 m; NP150: 1La, alt. 2470 m.

Paramerina sp.

The two-segmented maxillary palpus (Fig. 25) and the even teeth of the Li distinguish the genus.

Larva. A_1 striate, 248μ; CS,A_1 0.64 from base; AR 2.67; A_2 79μ; A_3 8 ; A_4 5μ; Bl 93μ ABl 92μ; Bl_2 10μ (Fig. 28); SP_2 (Fig. 28) 4μ; Bl/A_{2-4} 1.00; ABl/Bl 0.99; MD 100μ, apex in Fig. 27; A_1/MD 2.48; P_1 (Fig. 25) 15μ; P_2 35μ; CS, P, indistinct, between segments; P_b two-segmented; Li (Fig. 26) 75μ; $I_t$and M_t subequal to outer teeth; Pl (Fig. 26) 41μ; PH with 13-14 teeth; Pc 82μ with seven apical setae; L/W 2.67; TA elongate-conical, 163μ; L/Max. W 5.50; PP with 14 pale, simple claws.

SPECIMENS EXAMINED. NP 150: 1La, alt. 2470 m.



FIGS. 8-19. 8-10, larval Li: 8, *Thienemannimyia* sp.; 9, *Conchapelopia* sp.; 10, *Arctopelopia* sp. with Pl and PH; 11. *Arctopelopia* sp. 12-14, lateroventral setae and CS of MD; 12, *Thienemannimyia* sp.; 13. *Conchapelopia* sp.; 14, *Arctopelopia* sp.; 15-17, P_1 and P_b, larva. 15, *Thienemannimyia* sp.; 16, *Conchapelopia* sp.; 17, *Arctopelopia* sp. 18-19, apex A_1 and A_{2-4}, larva: 18, *Thienemannimyia* sp.; 19, *Arctopelopia* sp.

Genus nr. **Zavrelimyia** sp.

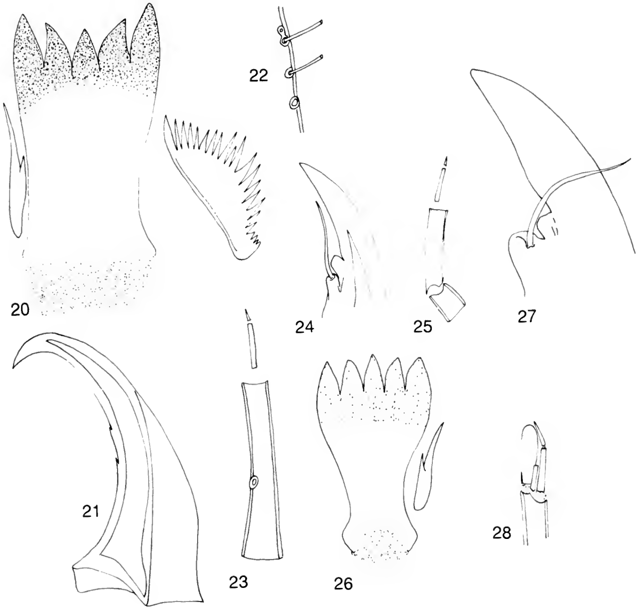
The single specimen is tentatively placed here on the basis of the large inner spur on one claw of the PP (Fig. 39) and the even length of the teeth of the Li (Fig. 38). It differs in the more sessile SP_2 (Fig. 36) a condition found in *Monopelopia, Xenopelopia, Pentaneurella,* and *Telmatopelopia.*

Larva. A_1 333m, faintly longitudinally striate; CS, A_1 0.62m from base; AR 3.43; A_2 80μ (Fig. 35); A_3 9μ; A_4 6μ; Bl and ABl, (Fig. 35) subequal, 94μ; Bl_2 15μ; SP_2 blunt, sessile on A_2 (Fig. 36) 7μ; Bl/A_{2-4} 0.97; MD 152μ; apex as in Fig. 34; A_1/MD 2.19; P (Fig. 37) 55m; CS, P_1 0.66 from base; A_1/P_1 6.05; Li 93μ; I_t and M_t (Fig. 38) equal to 0 teeth of Li; Pl as in Fig. 38; PH with 16 teeth; Pc 167 μ with seven apical setae; L/W 3.5; one of pale claws on PP with inner spur (Fig. 39).

SPECIMENS EXAMINED. NP122:1La, alt. 5860 m.

Nilotanypus sp. 1

This is a typical member of the genus with the characteristic Li (Fig. 31) and the one strongly



FIGS. 20-28. 20-24, *Trissopelopia* sp., larva: 20, Li and Pl; 21, Claw of PP; 22, lateroventral MD setae and CS, MD; 23, P_1 and Pb; 24, apex of MD. 25-28, *Paramerina* sp., larva. 25, $P_{1,2}$ and P_b; 26, Li and Pl; 27, apex of MD; 28, apex of antenna.

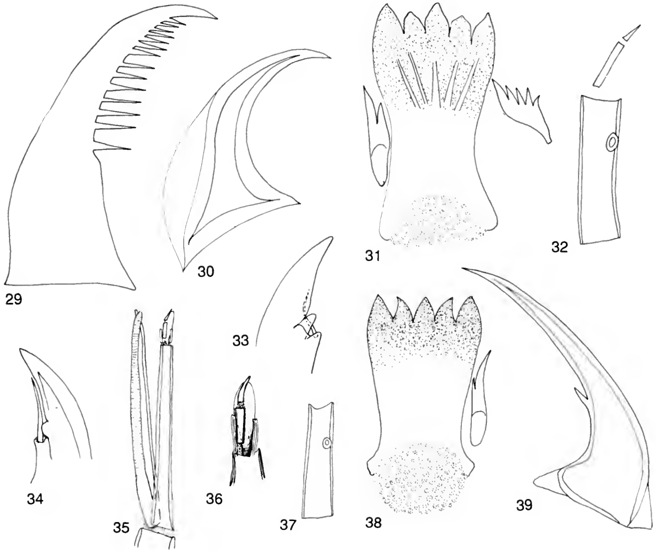
pectinate claw of the PP, resembling *N. fimbriatus* (Walk.)

Larva. Head 461μ L x 250μ W; A_1 167-181 ; CS,A_1 0.69-0.71 from base; AR 2.51; A_2 56μ; A_3 9 ; A_4 5μ; Bl 72μ; ABl 66μ; Bl_2 10μ; SP_2 4μ; Bl/A_{2-4} 1.00; ABl/Bl 0.92; MD 61-63μ, apex as in Fig. 33; A_1/MD 274-2.97; P_1 (Fig. 32) 28-29μ, L/W 3.8-4.0; CS, P_1 0.61-0.70 from base; P_b two-segmented A_1/P_1 596-6.46; Li (Fig. 31) 33-44μ ; I_t/O 0.95; M_t/O 0.98-1.03; PL as in Fig. 31; PH five-toothed (Fig. 31); Pc 88-95m, L/w 4.29-4.64; seven apical setae on Pc; TA tapering, 370μ; SBS simple; PP with 14 claws, one pectinate (Fig. 29); other claws with distinct outer flange (Fig. 30).

SPECIMENS EXAMINED. NP26: 2La, alt. 2250 m; NP38: 1La, alt. 2520 m.

Nilotanypus sp. 2

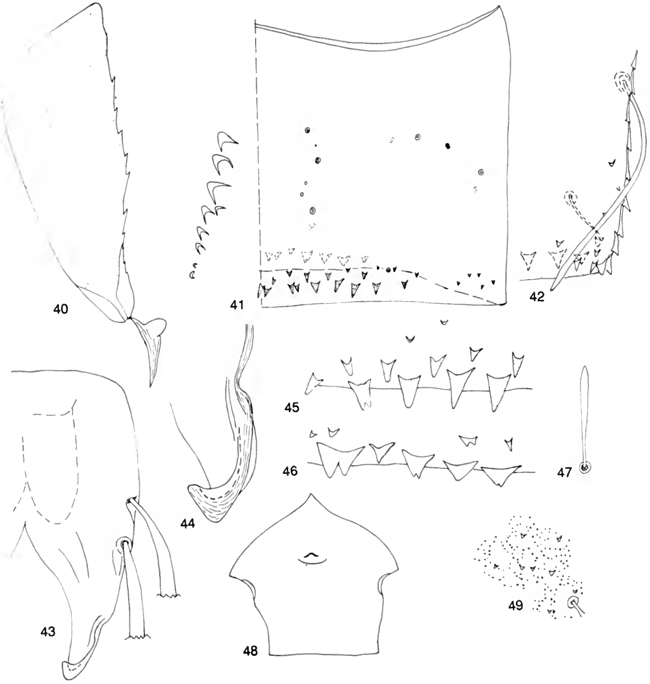
This taxon is represented by a single female pupa. The structure of the AL (Fig. 43) with the



FIGS. 29-39. 29-33, *Nilotanypus* sp., larva: 29, comb claw of PP; 30, flanged claw of PP; 31, Li, Pl and PH; 32, P_1 and P_b; 33, apex of MD. 34-39, Genus nr. *Zavrelimyia* sp., larva: 34, apex of MD; 35, apex of antenna; 36, detail of A_{3-4}, Bl_2, SP_2; 37, Pl; 38, Li and Pl; 39, toothed claw of PP.

apically on the abdominal segments are typical for the genus. Fittkau (1962) has described these for the European *N. dubius* (Meigen) and Roback (1986) for the North American species. The RO (Fig. 40) is considerably different from any known *Nilotanypus* pupa—it appears to lack a clear area and is irregularly shaped. It cannot be associated with *Nilotanypus* sp.1.

Pupa. FA as in Fig. 48; RO as in Fig. 40; PLP and clear area not discernible; RA appears to fill the RO; large tubercle at base of RO (Fig. 40); thoracic comb (Fig. 40) of 8-9 blunt tubercles; thorax brown; WP brown, veins only very faintly indicated; abdomen pale brown, no clear pattern; scar A.I., pale, posteriorly expanded; D, L and V setae A.IV arranged as in Fig. 41; D1 A.IV 18m, slightly expanded with blunt tip (Fig. 47); no apical spines on A.I.; A.II with an irregular double row of apical spines dorsally, none ventrally; A.III with irregular double row dorsally, shorter row ventrally; ventral spines paler; A.IV-VI with both dorsal and ventral apical rows; spines (Figs. 45, 46) about 7-10m; dorsal spines generally longer and darker than ventrals; A.VII with dorsal and ventral apical spine rows, about 0.5 segment width; ventral spines appear darker;



FIGS. 40-49. *Nilotanypus* sp. 2, pupa: 40, RO and thoracic comb; 41, setal pattern, spines of A.IV; 42, caudolateral corner A.VII; 43, AL; 44, detail, apex of AL; 45, detail, apicodorsal spines A.IV; 46, detail, apicoventral spines A.IV; 47, seta D_1, A.IV; 48, FA; 49, shagreen A.IV near D_2.

A.VIII with 7-8 pale ventral spines on each side, none dorsally; shagreen (Fig. 49) of tergites of short spines, about 1.5 μ L and scattered dark points; A.VII with one LS (Fig. 42) 0.66 from base of segment; A.VIII with five LS at 0.48, 0.66, 0.81, 0.93, 1.00 segment length; AL with blunt recurved tip (Fig. 44); 167m L; LS, AL at 0.44, 0.58 from base of AL; almost longitudinally aligned in position; do not appear to have sticky sheaths; female GS 0.49 AL-L.

SPECIMENS EXAMINED. NP5: 1 female PEx, alt. 1046 m.

Subfamily DIAMESINAE

With the single exception of *Pseudodiamesa nepalensis*, the diamesine taxa reported here were identified exclusively from immature stages. Four genera are represented with a combined total of nine species. These taxa were collected over an altitudinal range of 3725 m (2135 m - 5860 m). Diamesine taxa were collected at only 12 sites and were never very diverse: 10 sites had only 1 species and 2 sites had 2 species.

Boreoheptagyia sp.

Only one early instar larva of this *Boreoheptagyia* species was found. Unfortunately, it is in very poor condition. However, many diagnostic features are visible. It agrees with the generic diagnosis of Oliver (1983) in the structure of the labrum, Pm, M and body. The maxilla is not visible. Points of difference are the antenna which has the 3rd segment much longer than the 2nd (Figs. 50-51), the long SSd of the MD which almost reaches the tip of the apical tooth (Fig. 52) and the dorsal surface of the head which appears to have only two tubercles (Fig. 53). Gut contents - very fine detrital particles and a large number of small brown spheres (spores?).

SPECIMENS EXAMINED. NP 75: 1La (III?), alt. 3475 m.

Genus **Diamesa**

It is not surprising that this montane genus is well represented in the Nepalese material. Four species are recognized, three from larvae alone and one from associated larvae and pupae. The four species recorded here are apparently all different from those described by Saether and Willassen (1987) from Nepal.

Diamesa cf. aberrata Lundbeck:

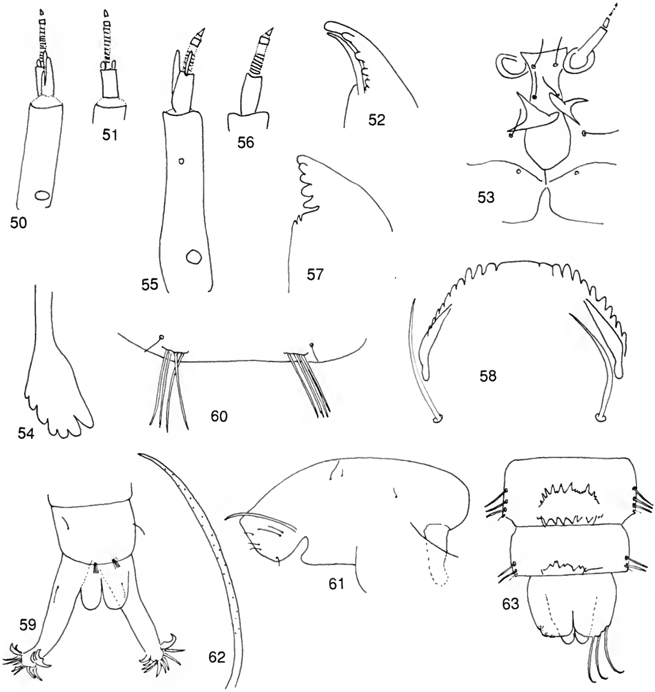
Diamesa aberrata Lundbeck 1898: 289

This is the most common of the four *Diamesa* species found. Larvae, prepupae, pupae and pupal exuviae are included in the material. The pupa agrees very closely with *D. aberrata* Lundbeck as described by Serra-Tosio (1971). This species is known to have an extensive Holarctic distribution. Gut contents - small detrital particles and small diatoms.

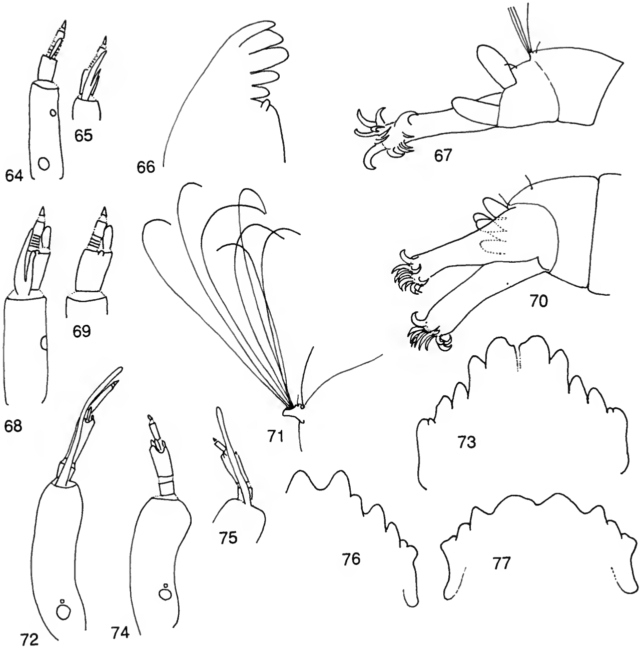
Pupa. Large FS on FA; RO with small spinules on surface (Figs. 61-62); thoracic chaetotaxy: 3 MAps, 1 LAps, 2 Pcs and 3 Dcs (Fig. 61); abdominal chaetotaxy, armature and AL as in Fig. 63.

Larva. About 7 mm in length (4th instar); head dark reddish-brown, PO black; S.I simple and strong, other labral setae and chaetae as typical of genus; PM with 7-8 teeth (Fig. 54); antenna with 5 segments (Figs. 55-56); MD broad with apical tooth and 4 inner teeth moderately long (Fig. 57), SSd and Si present, Si with many branches; M with a simple median tooth and 11 pairs of lateral teeth, median and first and second lateral teeth often worn to form a median bar (Fig. 58); abdomen dark with all setae small; Pc very much reduced (absent?) with 4 very short setae (Figs. 59-60). The larva from NP119 appears to have a small rounded median tooth of the M and only 10 pairs of lateral teeth. The MD of this larva has the apical tooth longer than any of the inner teeth.

SPECIMENS EXAMINED. NP37: 7La, 1 PrP, 4 male, 1 female P, 1 male, 2 females, 1 P,1, 2PEx, alt. 2480 m; NP119: 1La, alt. 4760 m; NP 121: 1 female PEx, alt. 4985 m; NP134: 1La, 1 PrP, 1 female P, alt. 3500 m.



FIGS. 50-63. 50-53, *Boreoheptagyia* sp.: 50, antenna with Bl; 51, flagellum of antenna without Bl; 52, apex of MD with SSd; 53, dorsal surface of head. 54-63, *Diamesa* cf. *aberrata*: 54, Pm; 55, antenna, with Bl and style; 56, flagellum of antenna without Bl and style; 57, apex of MD; 58. M: 59, anal segments of larva, dorsal; 60, "procercal" setae; 61, RO and thoracic chaetotaxy; 62, RO; 63, A.VII-VIII and AL, dorsal.



FIGS. 64-77. 64-66, *Diamesa* sp. 1: 64, antenna without Bl; 65, flagellum of antenna with BL; 66, apex of MD; 67, *Diamesa* sp. 2: 67, anal segments of larva, lateral. 68-70, *Diamesa* sp. 3: 68, antenna with Bl; 69, flagellum of antenna without Bl; 70, anal segments of larva, lateral; 71, *Pagastia* sp. 2: 71, Pc. 72-73, *Brilla modesta* gr. sp.: 72, antenna; 73, M, 74-77, *Brillia* sp.: 74, antenna without Bl; 75, flagellum of antenna with Bl; 76, M, partial; 77, M with worn median teeth.

Diamesa sp. 1

The larvae placed in this taxon were all collected at NP 114 and are the only *Diamesa* larvae from that site. The larvae are all small (about 3.5mm) and may represent a small species or an early instar of a larger species. In most respects these larvae are very similar to *D*. cf. *aberrata*, differing only in antennal proportions, which are probably related to instar (Fig. 64-65), the long teeth of the MD (Fig. 66) and the lack of dark pigmentation of the setae of the Pc. Given the absence of typical *D*. cf. *aberrata* larvae from this station and the differences in the MD, it is probably best to treat these larvae as a separate species. Gut contents - small detrital particles and diatoms.

SPECIMENS EXAMINED. NP114: 5La (III?), alt. 4640 m.

Diamesa sp. 2

A single larva of this taxon was found at NP 37, the station where most of the *D*. cf. *aberrata* specimens were collected. This small larva (about 4mm) could be an early instar of *D*. cf. *aberrata*. However, it differs from 4th instar *D*. cf. *aberrata* in the following characters: the MD has long teeth as in *D*. sp. 1, the antenna has the proportions of the antenna of *D*. sp. 1 and the setae of the Pc are much longer than those of *D*. cf. *aberrata* (Fig. 67). The last difference probably has more significance than the first two and it is felt that separation of this larva is justified. Gut contents - small detrital particles and diatoms.

SPECIMEN EXAMINED. NP3: 1La (III?), alt. 2480 m

Diamesa sp. 3

This is the most distinctive of all the *Diamesa* species found in the Nepalese material. Two larvae are placed here. Both may be 3rd instar. This species differs from all of the other *Diamesa* species by the presence of only a single weak seta on the "procercus" (Fig. 70). All of the other species have 4. The antenna of this species is small, very darkly pigmented and has a very large and dark style (Figs. 68-69). The labrum of this species is also different from the other *Diamesa* species in that there appear to be no additional chaetulae lateral to the CHM and LL. The M of both specimens is broken. The MD has teeth intermediate in length to those of *D*. cf. *aberrata* and *D*. sp. 1. Gut contents - small detrital and inorganic particles.

SPECIMENS EXAMINED. NP 90: 1La (III?), alt. 4025 m; NP103: 1La (III?), alt. 4250 m.

Pagastia sp. 1

Only one larva of this taxon was found. Unfortunately, it is in poor condition, but in all observable structures it fits the description of *Paqastia* sp. A (Oliver and Roussel, 1982). Gut contents - detritus and diatoms.

SPECIMEN EXAMINED. NP 23: 1La (III?), alt. 2135 m.

Pagastia sp. 2

Larvae assigned to this species agree in most details with *P. partica* (Oliver and Roussel 1982). The differences between these two species include: the lack of dark markings on the head of *P*. sp. 2; the antenna of *P*. sp. 2 is about 3/4 the length of the MD (1/2 for *P. partica*); the Pc of *P*. sp. 2 has 7 setae, not 8 as in *P. partica* (Fig. 71); and the basal lateral seta of the Pc of *P*. sp. 2 is much stronger than that of *P. partica* (Fig. 71). Gut contents - detritus and diatoms.

SPECIMENS EXAMINED. NP15: 3La (III?), alt. 2470 m.

Pseudodiamesa sp. 1

A prepupa of this species was collected at NP 47. The specimen is about 9mm in length and has many of the head structures obscured. Based on the simple S.I of the labrum (possibly absent) and the Pc having 7 setae, this specimen should be placed in the subgenus *Pseudodiamesa* (Oliver 1983). However, the developing pupa has all of the lateral setae of A.VI-VII simple, which is characteristic of the subgenus *Pachydiamesa* (Oliver in press). This matter is made even more confusing when the character conflict of the larva and pupa of *Pseudodiamesa nepalensis* Reiss is considered. Gut contents - empty.

SPECIMEN EXAMINED. NP4: 1PrP, alt. 2660 m.

Pseudodiamesa nepalensis Reiss

Pseudodiamesa nepalensis Reiss 1968:60

A mature larva and 6 pupal exuviae of this species were taken at NP150 and several males, some with associated pupal exuviae, were found at NP 124. The larva is quite large (about 17 mm in length). It has pectinate S.I and 8 setae on the Pc, both of which are character states of the subgenus *Pachydiamesa*. However, all of the large (about 12mm in length) pupal exuviae taken at the same station have the L1 and L3 setae of A.VI-VII and L2 of A.VIII branched (at least, bifid). Branched lateral setae are characteristic of the subgenus *Pseudodiamesa* (Oliver 1986). The male adults from NP124 are most probably *Pseudodiamesa nepalensis* Reiss. Neither the larva nor the pupa of *P. nepalensis* was described by Reiss (1968). It is possible that the conflict between the larva and pupa-adult of this taxon is due to an error in the association of the larva with the other two stages. Gut contents - detritus and a few diatoms.

SPECIMENS EXAMINED. NP124: 3 male P, 1 female P, 6 male A, alt. 5860 m; NP150: 1La, [COF] 6 male PEx; [COF] alt. 2470 m.

Subfamily Orthocladiinae

All of the orthoclad taxa were determined from immature stages only. A total of 50 species were collected and these are assignable to 24 named genera and one, apparently, new genus. The Orthocladiinae were collected over an elevational range of 3929 m (1046-4975 m), but most occurred between 2000 and 3500 m. Orthoclads are recorded from 52 of the 69 localities that yielded chironomids.

Brillia flavifrons gr. sp.

Six larvae from 3 stations are placed in this species. These specimens agree very closely with the description of the *flavifrons* group (Oliver and Roussel 1983) in the following characters: Cl weakly sclerotized, Sl_2 divided into 3 parts with the posterior pair narrowly separated; Bl slightly longer than flagellum and the M with 4th lateral tooth larger than the 5th. The only exception to the agreement with the *flavifrons* group is the absence in some of the larvae of the dark spot between the eyespot and the base of the antenna and MD. Gut contents - plant tissue (wood or leaves).

SPECIMENS EXAMINED. NP16: 2La (III), alt. 1610m; NP26: 2La (1 III, 1 IV), alt. 2250 m; NP 83-1La, alt. 3770 m.

Brillia modesta gr. sp.

Three larvae of this species were found in material from 2 stations at relatively high altitudes. They represent a typical *modesta* group species but differ from the description of the *modesta* group in Oliver and Roussel (1983) by having the Bl slightly longer than the flagellum (Fig. 72), and by the prominent first lateral tooth of the M (Fig. 73). Gut contents - plant tissue (wood or leaves).

SPECIMENS EXAMINED. NP85: 2La, alt. 3900 m; NP89: 1La, alt. 3995 m.

Brillia sp.

Two 4th instar larvae are placed in this unusual *Brillia* species. It does not fit well into either the *modesta* or the *flavifrons* groups, but appears to be most similar to the *flavifrons* group. The M, however, is most similar to the *modesta* group. Gut contents - mixture of fine organic detritus and plant tissue.

Larva. About 10mm in length (4th instar);

head yellow, PO behind PM pale, dark laterally; Cl strongly sclerotized with SI_2 divided into 5 parts; antenna with 5 segments, LO small, Bl longer than flagellum, relative lengths of the segments unusual (Figs. 74-75); M with 4th and 5th lateral teeth partially fused (Fig. 76), in worn specimen it appears as if there are only 4 lateral teeth (Fig. 77); MD with basal tooth not appressed to Mo; other structures as in *flavifrons* group.

SPECIMENS EXAMINED. NP5: 1La, alt. 2675 m; NP76: 1La, alt. 3495 m.

Chaetocladius dentiforceps gr. sp.

A larva, one larval exuviae and two pupal exuviae from NP37 are placed in this taxon. Gut contents - detritus particles.

Pupa. Length about 5.5mm, pale yellow; FS on FA, no tubercles or warts on FA; thoracic chaetotaxy as in Fig. 83, includes a distinct Mns seta (often present in *Chaetocladius*); RO strongly sclerotized, golden, with small spinules on distal 3/4 (Figs. 83-84); dorsal shagreen: A.I with extensive shagreen, bare only in anteromedian area, spinules small; A.II-IV with a weak longitudinal median band; A.V-VIII with shagreen on most of surface; dorsal spine groups: A.II-VIII with posterior rows of moderately long spines (Figs. 85-86); chaetotaxy: A.II-VII with two spine-like and two hair-like lateral setae (Fig. 85), A.VIII with only hair-like lateral setae (Fig. 86); AL with three very short, thorn-like AM? which often have weak lateral denticles (Figs. 86-87), AM evenly or unevenly spaced along AL margin.

Larva. About 7mm in length (4th instar); head orange-brown, MD, M and PO darker; S.I apparently simple, perhaps with one lateral branch, LL large but simple, all chaetae apparently simple, spines of PE narrow and subequal (Fig 78); Pm simple, weak PmB may be present; antenna with 5 segments, LO moderately large, Bl reaches almost to apex of 4th antennal segment (Figs. 79-80); MD typical, with SSd and Si; M with domed median tooth and 5 pairs of lateral teeth, VmP large (Fig. 81); PG of maxilla apparently absent; abdomen slender, with distinct bluish pigment, all setae small; Pc moderately developed with 7 setae, claws of PP brown-yellow, TA long and with several constrictions (Fig. 82).

SPECIMENS EXAMINED. NP37: 1La, 1LEx, 2 female PEx, alt. 2480 m.

Chaetocladius vitellinus gr. sp.

Two larvae are placed in this taxon. Gut contents - small detritus and diatoms.

Larva. About 6.5mm in length (4th instar); head orange-yellow, MD, M and PO darker; S.I with multiple branches, LL with about 4 apical teeth, some CHM serrate (Fig. 88), ChL simple?, 3 spines of PE narrow and subequal; Pm with 2 apical teeth and 1 lateral tooth, weak PmB present (Fig. 89); antenna with 5 segments, LO moderately large, Bl reaches middle of 3rd segment (Fig. 90); MD with apical tooth and 3 lateral teeth, SSd and Si present; M with a single median tooth, but with 2 peaks, VmP moderately large (Fig. 91); maxilla with PG distinct; abdomen slender and yellow, all setae small; Pc strong, partially sclerotized and with 6 setae; claws of PP simple and brown; TA about 1/2 length of PP (Fig. 92).

SPECIMENS EXAMINED. NP42: 1La, alt. 2520 m; NP127: 1La, alt. 3500 m.

Corynoneura cf. **lobata** Edwards

Corynoneura lobata Edwards 1924: 186.

Larvae of this species were found in the collections from 8 stations. The larva fits *C. lobata* very closely. Gut contents - fine detritus.

SPECIMENS EXAMINED. NP8: 7La, alt. 1530 m; NP12: 1La, alt. 1462 m; NP14: 3La, alt. 1548 m NP16: 1La, alt. 1610 m; NP 25: 1La, alt. 2180m; NP26: 4La, alt. 2250 m; NP 38: 2La (1-III, 1-IV), alt. 2520 m; NP83: 1La (II), alt. 3770 m.

Cricotopus (C.) bicinctus gr. cf. **vierriensis** Goetg.

Cricotopus vierriensis Goetghebuer 1935: 417418.

Three larvae and a prepupa are placed in this taxon. All of the larvae key directly to *C. vierriensis* in Hirvenoja (1973) however, abdominal setal tufts are visible on only one larva (NP33). One of the larvae from NP18 has characters that differ from the other specimens and may represent a second species that keys to *C. vierriensis*. In this specimen, the antennal proportions are different, the M has a less wide median tooth, the Pm is broader and the maxilla has no pectinate lamellae on the galea. The abdomen of this specimen has a light violet tint in contrast to the greenish-yellow color of the other specimens. The antenna, M, Pm and maxilla of the two forms are compared in Figs. 93-96, 98-101. Gut contents - mixture of detritus and diatoms. Based on larval head characters, the prepupa appears to belong to this taxon. No abdominal setal tufts are visible. The developing pupal integument is partially visible and is not inconsistent with *C. vierriensis* in size and arrangement of dorsal spinule groups on A.II-VI. However, the presence of spinule groups on A.VII and VIII does not fit *vierriensis*. No RO could be seen, probably because of the poor condition of the specimen. The lateral setae of A.VII-VIII of the pupa are unusually large for any species of *Cricotopus* known to me (Fig. 97).

SPECIMENS EXAMINED. NP18: 2La, alt. 2000 m; NP33: 1La, alt. 2390 m; NP144: 1PrP, alt. 2300 m.

Cricotopus tremulus gr. cf. **curtus** Hirvenoja

Cricotopus (Cricotopus) curtus Hirvenoja 1973: 199

A single larva of this species was found. It keys directly to *C. curtus* in Hirvenoja (1973) and fits the description in all visible details. Gut contents - small diatoms.

SPECIMEN EXAMINED. NP33: 1La, alt. 2390 m.

Eukiefferiella brehmi gr. sp.

Larvae of this species were found in collections from 6 stations. They agree in all details with the description of Nearctic representatives of the *brehmi* group (Bode, 1983). Gut contents - mixed detritus and diatoms.

SPECIMENS EXAMINED. NP 5: 2La, alt. 1046 m; NP8: 3La (1-III, 1-IV), alt. 1548 m; NP14- 2La (I-III, I-IV), alt. 1548 m; NP18: 2La, alt. 2000m NP26: 1La, alt. 2250 m; NP 38: 2La (1-III, 1-IV), alt. 2520 m.

Eukiefferiella claripennis gr. sp.

This is a typical *E. claripennis* group species. The M has a median pair of narrow teeth and the antenna has 4 segments. The single prepupa, which has only partial development of pupal characters, indicates that placement should be in or near brevicalcar and its allies. The TH is too large for *claripennis* (Fig. 102). The wide gap between the lateral groups of conjunctive Hl also indicates placement in or near *E. brevicalcar*. Gut contents - fine detritus and small diatoms.

SPECIMENS EXAMINED. NP18: 1La (II), alt. 2000 m; NP26: 1PrP, alt. 2250 m; NP 38: 2La (1-II, 1-IV), alt. 2520 m; NP91: 1La, alt. 4050 m; NP 139: 2La, alt. 4100 m; NP 150: 1La (III), alt. 2470 m.

Eukiefferiella devonica gr. sp.

A single larva is placed in this taxon. It appears to be a typical *devonica* group species with a short, squat head, a 5 segmented antenna and a M with a single wide median tooth and only 4 pairs of lateral teeth. The abdomen is pale yellow-green with very contrasting salivary glands (dark red-brown). Gut contents - diatoms and plant tissue.

SPECIMEN EXAMINED. NP18: 1La, alt. 2000 m.

Eukiefferiella gracei gr. cf. gracei (Edwards)

Spaniotoma (Orthocladius) gracei Edwards 1929
Eukiefferiella gracei: Saether & Halvorsen 1981: 280.

This is a common species in the material available. Based on larval and pupal characters it seems to fit *E. gracei* very well. The larva and pupa are associated in a mature prepupa. The color of the abdomen varies from pale violet to deep purple. The darkest specimens are both from NP14 and are also characterized by a somewhat narrower median tooth to the M and less distinct LO. These specimens may represent a second species near *E. gracei*. The 3 very immature prepupae from NP 83 are only 2mm in length (vs. 3mm for the prepupa and pupa from NP 90), but otherwise seem to be identical to *E. gracei.* Gut contents - detritus and diatoms.

SPECIMENS EXAMINED. NP8: 1La, alt. 1530 m; NP14: 2La, alt. 1548 m; NP16: 2La (1-III, 1-IV), alt. 1610 m; NP 17: 1La, alt. 1660 m; NP 25: 1La (III), alt. 2180 m; NP38-1La, alt. 2520 m; NP47: 1La, alt. 2660 m; NP83: 3PrP, alt. 3770 m; NP89-1La, alt. 39945 m; NP90: 1La, 1PrP, 1 P, alt. 4025 m; NP98-05La, alt. 4100 m; NP150: 1La, alt. 2470 m.

Eukiefferiella rectangularis gr. sp.

A single larva taken from a glacial moraine stream is assignable to the *rectangularis* group. The *rectangularis* group of *Eukiefferiella* has recently been moved to the redefined genus *Tokunagaia* (Halvorsen and Saether, 1987). This species may be identical with their *T.* sp. A based on pupal exuviae from Darjeeling. Gut contents - inorganic particles and diatoms.

Larva. Length 3.5mm; head dark reddish-brown, PO darker; antenna with 5 segments, LO moderately large, BL reaching apex of 3rd segment (Fig. 103); S.I simple, other labral characters obscured; MD broken, with 2 long serrations on inner margin; M with a pair of broad, squared median teeth and 5 pairs of lateral teeth (Fig. 104); abdomen and thorax with most setae small - largest about 1/3 the length of a segment; abdomen dark greyish-blue.

SPECIMEN EXAMINED. NP 98: 1La, alt. 4100 m.

Eukiefferiella sp.

Four larvae from 3 stations are placed in this species. It does not seem to fit well in any established group of *Eukiefferiella*, but comes closest to *E. claripennis* and *E. coerulescens* . The M is very similar to that of Eukiefferiella sp. D of Cranston (1982a). The yellow head capsule is unusual for *Eukiefferiella* as is the long antenna. Gut contents - small detritus and a few diatoms.

Larva. Length about 4mm (probably 4th instar); head yellow, PO, MD and M brown; antenna about 1.5x the length of the MD, 5 segments, LO very large, Bl about equal to segment 2 (Fig. 105); labral structures not visible; MD normal; M with a narrow, somewhat peaked, median tooth and 5 pairs of lateral teeth (Fig. 106); abdomen greenish-yellow, all abdominal setae very small.

SPECIMENS EXAMINED. NP26: 1La, alt. 2250 m; NP136: 1La (II), alt. 2135 m; NP144: 2La (1-III, 1-IV), alt. 2300 m.

Heleniella sp.

Three larvae and a pupa, all from different stations, are assigned to this species. The larva generally fits the diagnosis of *Heleniella* in Cranston et al (1983), but differs in specific details. The unassociated pupa also appears to be *Heleniella*, but like the larva, differs from any described species. It is possible that the larva and pupa do not belong to the same species. Gut contents - coarse plant tissue.

Pupa. About 4.5mm in length; small FS on FA, no warts or tubercles; RO with numerous spinules, almost to base (Figs. 111- 112); thoracic chaetotaxy (Fig. 111); dorsal shagreen: A.I-VIII absent; dorsal spine groups A.II-VIII with a posterior row of blunt to sharp spines, largest on A.IV and A.V (Fig. 113); apparently no conjunctive with transverse band of spinules; ventral spine groups: A.II and A.III with anteromedian groups of long needle-like spines, extending laterally on A.II; A.IV- VIII (male) with a row of large, sharp spines on the posterior margin (Fig. 114); AL in poor condition, apparently narrow with 3 terminal AM; partially developed male genitalia with very weak anal point.

Larva. Length about 5mm (4th instar); head yellow, PO pale, MD and M brown; S.I with apical points, a pair of weak LL between bases of S.I (Fig. 107); Pm with 2 apical teeth (Fig. 108); antenna apparently with only 4 segments, segment 2 with typical basal section set off from longer distal section , LO small, Bl much longer than flagellum (Fig. 109); M typical of *Heleniella* (Fig. 110); maxilla not visible.

SPECIMENS EXAMINED. NP26: 1La, alt. 2250 m; NP50: 1male P, alt. 2710 m; NP93: 1La, alt. 4090 m; NP100: 1La, alt. 4155 m.

Krenosmittia sp.

A single larva, with head missing, was found in the collection from NP26. It has the typical long seta on the Pc and the long slender body form of *Krenosmittia*. It is possible that it should be placed in *Pseudorthocladius*. No larvae of *Pseudorthocladius* and no pupae of either genus were found at any station. Gut contents - empty.

SPECIMEN EXAMINED. NP26: 1La (IV?), alt. 2250 m.

Limnophyes sp.

This species is based on one larva, a prepupa and two pupae. The larvae fit the general diagnosis of *Limnophyes* as given in Cranston et al (1983), but differ in a few details. S.I multibranched, almost plumose, and the PE consists of 3 spines, the middle one much shorter (Fig. 115). The Pm has a definite brush (Fig. 115). The statement in Cranston et al. (1983) that only some Nearctic species of *Limnophyes* have a PmB is in error (O.A. Saether pers. comm.). Gut contents - coarse detritus.

The pupae are typical *Limnophyes*. One of the few useful characters for separating some species of *Limnophyes* is the length of the AM of the AL. In this species the AM are long (Fig. 116).

SPECIMENS EXAMINED. NP18: 1PrP, alt. 2000 m; NP26: 2 male P, alt. 2250 m; NP37: 1La, alt. 2480 m.

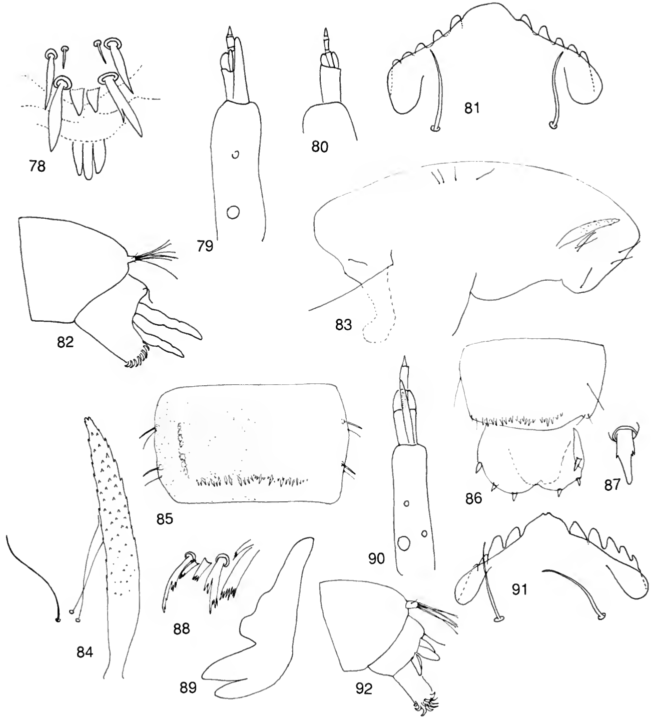
Metriocnemus hygropetricus gr. sp.

Larvae, pupae and a pupal exuviae of this species were found. Although the larva and pupa are not directly associated, all the pupae and the pupal exuviae were collected at NP37 where most of the larvae were found. Both the larva and the pupa key to the *hygropetricus* group. Gut contents - detritus, sometimes distinct pieces of plant tissue.

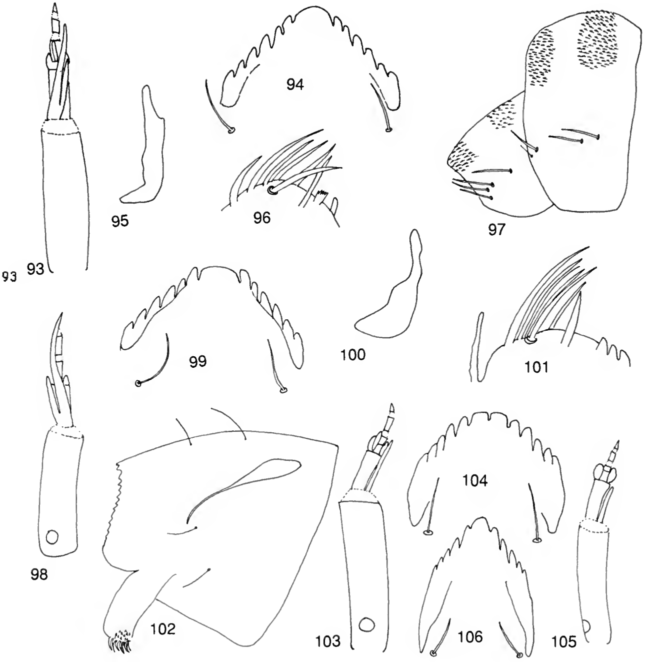
Pupa. FS absent; RO absent; all setae of the thorax weak, 2 MAps, 3 Pcs, 4 Dcs (all close together); abdomen with strong Apo on dorsal and ventral surfaces of A.II-VIII; dorsal shagreen: A.I-II absent, A.II-III with anteromedian groups of fine spines, most conjunctives with very weak anteriorly directed spinules in several rows on dorsal surface and continuing laterally where the spinules are stronger and on to the ventral conjunctive where the spines are the strongest; dorsal spine groups: A.III-VIII with a single row of closely-set, blunt spines across posterior margin (Fig. 121); AL with two small but distinct "macrosetae" (Fig. 121).

Larva. About 6 mm in length (4th instar); head dark brown; S.I plumose, LL pectinate, Pm bifid, brush distinct (Fig. 117); antenna with 5 segments (Fig. 118); MD as in Cranston et al (1983, Fig. 9.43A); M with recessed median pair of teeth and 5 pairs of lateral teeth (Fig. 119); abdomen and thorax strongly but irregularly pigmented dark purple; Pc with a strong spur, TA long (Fig. 120).

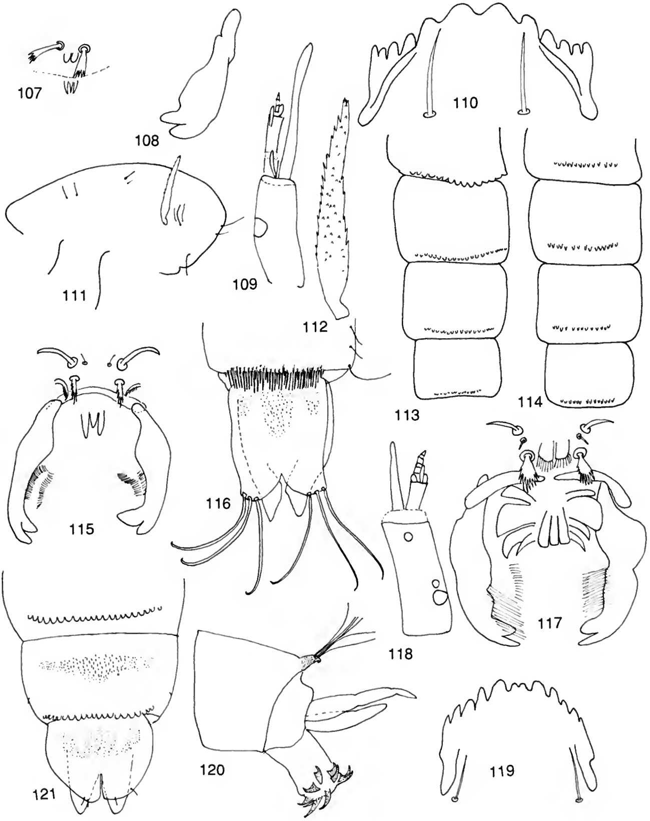
SPECIMENS EXAMINED. NP37: 8La, 2 male, 1 female P, 1 female PEx, alt. 2480 m; NP47: 1La, alt. 2660 m; NP150: 1La, alt. 2470 m.



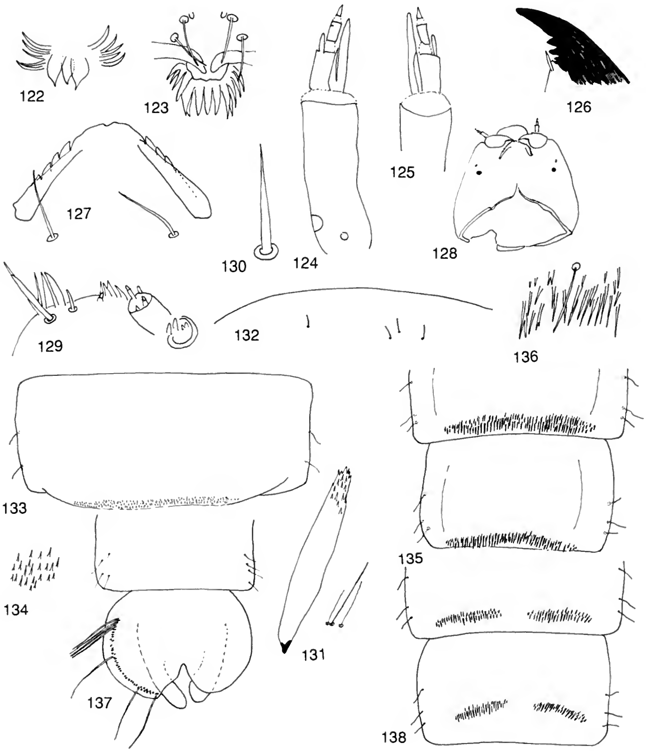
FIGS. 78-92. 78-87, *Chaetocladius dentiforceps* gr. sp.: 78, labral setae and PE; 79, antenna with BL; 80, flagellum of antenna without Bl; 81, M; 82, anal segments of larva, lateral; 83, RO and thoracic chaetotaxy; 84. RO and Pcs; 85, tergum of A.V; 86, A.VIII and AL, dorsal; 87, basal "macroseta" of AL; 88-92, *Chaetocladius vitellinus* gr. sp.: 88, some labral setae and chaetae; 89, Pm; 90, antenna; 91, M; 92, anal segments of larva, lateral.



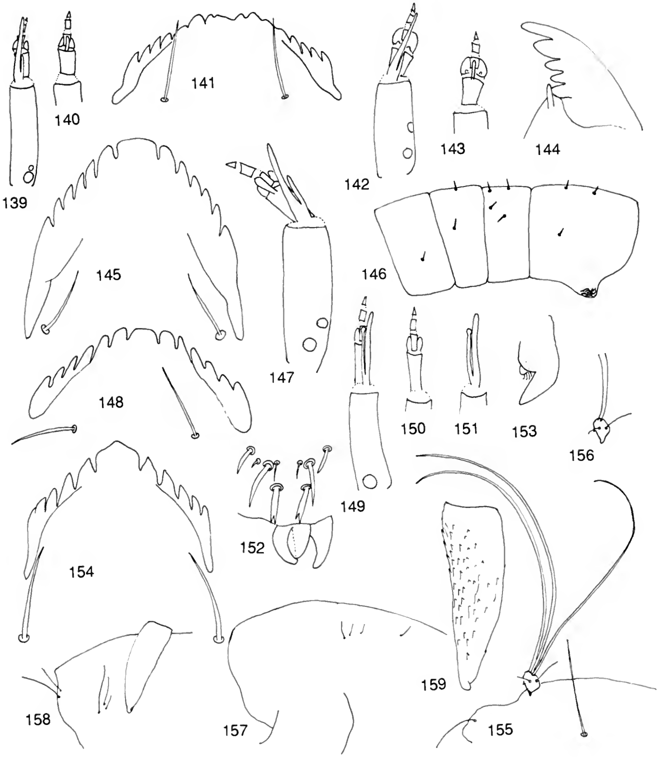
FIGS 93-106. 93-97, *Cricotopus* (*C.*) cf. *vierriensis*, form A: 93, antenna; 94, M; 95, Pm; 96, maxilla; 97, A.VII and VIII of developing pupa, lateral. 98-101, *Cricotopus* (*C.*) cf. *vierriensis*, form B: 98, antenna; 99. M; 100, Pm; 101, maxilla; 102, *Eukiefferiella claripennis* gr. sp.: 102, developing RO. 103-104, *Eukiefferiella rectangularis* gr. sp.: 103, antenna; 104, M; 105-106, *Eukiefferiella* sp.: 105, antenna; 106, M.



FIGS. 107-121. 107-114, *Heleniella* sp.: 107, S.I. LL and PE; 108, Pm; 109, antenna; 110, M; 111, RO and thoracic chaetotaxy; 112, RO; 113, terga A.V-VIII; 114, sterna A.V-VIII. 115-116, *Limnophyes* sp.: 115, labral setae, PE and Pm; 116, posterior margin of A.VIII and AL, dorsal. 117-121, *Metriocnemus hygropetricus* gr. sp.: 117, labral setae, epipharynx and Pm; 118, antenna; 119, M; 120, anal segments of larva, lateral; 121, A.VII-VIII and AL, dorsal.



FIGS. 122-138. 122, *Nanocladius (N.) parvulus* gr. sp.: 122, scales of PE. 123-138, *Nanocladius* (*P.*) sp.: 123, labral setae and PE; 124, antenna with partial division of 3rd segment; 125, antenna with undivided 3rd segment; 126, apex of MD; 127, M; 128, head, ventral; 129, maxilla; 130, "macrochaeta" of body; 131, RO and Pcs; 132, distribution of Dcs; 133, tergum A.III; 134, detail of posterior spinules of A.III; 135, terga A.VI-VII; 136, detail of spines of tergum A.VII; 137, A.VIII and AL, dorsal; 138, sterna A.VI-VII.



FIGS. 139-159. 139-141, *Orthocladius* (*Euorthocladius*) poss. *rivulorum* gr. sp.: 139, antenna with Bl; 140, flagellum of antenna without Bl; 141, M; 142-146. *Orthocladius* (*Euorthocladius*) sp. 2: 142, antenna with Bl; 143, flagellum of antenna without Bl; 144, apex of MD; 145, M; 146, thorax and first abdominal segment, lateral. 147-148, *Orthocladius* (*O.*) sp.: 147, antenna; 148, M. 149-159, *Paracricotopus* sp.: 149, antenna with Bl; 150, flagellum of antenna without Bl; 151, Bl of antenna. 152, labral setae and PE; 153, Pm and serrate lamellae; 154, M; 155, Pc with 3 strong setae; 156, Pc with strong setae removed; 157, distribution of Dcs; 158, anterior thorax and RO; 159, RO.

Nanocladius (N.) parvulus gr. sp.

This species is represented by 3 larvae from NP 38, none of which are in good condition. The species is typical of the *parvulus* group and comes quite close to the description of *N. rectinervis* (Saether 1977a). The only evident difference between this species and *N. rectinervis* is the larger size of the scales of the PE of this species (Fig. 122). Gut contents - all empty.

SPECIMEN EXAMINED. NP38: 3La, alt. 2520 m.

Nanocladius (Plecopteracoluthus) sp.

Two larvae and 2 pupae, associated with larval exuviae, were found on Perlidae nymphs of the genus *Kamimuria* taken at NP8. The larvae and pupae were encased in silken tubes on the ventral side of the thorax of the nymphs. The genus *Plecopteracoluthus* was described by Steffan (1965) and moved to *Nanocladius* as a subgenus by Saether (1977a). Until now, only 2 Nearctic species and 1 Neotropical species (Epler, 1986) were known. This species differs from the described species in both larval and pupal stages. Gut contents - very small detritus particles and small diatoms.

Pupa. About 5mm in length; exuviae light brown; FS not visible, if present; RO short, slightly narrower and darker at base, dense spinules at apex (Fig. 131); Pcs all weak, but of different sizes (Fig. 131); all Dcs small, Dcs1 much anterior of others (Fig. 132); shagreen apparently absent on all terga and sterna except for terga A.V-VI which have small median groups of moderately long, thin spinules; dorsal spine groups: A.II with a posterior band of small anteriorly directed spinules, extends across most of segment, probably on conjunctive; A.III-IV with similar posterior band as on A.II, but spinules somewhat larger (Figs. 133-134); A.V with 1-2 rows of moderately long, thin, posteriorly directed spines on posterior margin, extending along most of margin; A.VI-VII with spine rows as A.V, but 3-4 rows and spines longer (Figs. 135-136); A.VIII without spines (Fig. 137); ventral spine groups: A.I-III without spines; A.IV with a posterior row of posteriorly directed spines, row has a wide gap in the middle; A.V-VII with similar posterior row to that on A.IV, but spines longer and gap in middle smaller (Fig. 138); A.VIII without spines; PSA and PSB absent?; lateral chaetotaxy of abdomen: A.II-V with 2 weak lateral setae, A.VI-VII with 3 or 4 weak lateral setae (Fig. 133); A.VIII with 4 weak lateral setae (Fig. 137); AL brown except along the outer margin; fringe setae in 1-2 irregular rows (60-70 setae), no AM (Fig. 137); genital sheaths of male slightly longer than AL (Fig. 137); pharate male with genitalia structures similar to those of *P. downesi*, but definitely without anal point.

Larva. 5-6mm in length (4th instar); head short and broad, yellow with posterior darkening to orange-yellow, PO, MD, and M darker; S.I and other labral setae simple, no CHM, scales of PE narrow and subequal (Fig. 123); Pm with 2 long apical teeth; antenna with only 4 segments, but one antenna of one specimen has a partial division of segment 3, basal segment with irregular outline, LO absent?, Bl slightly shorter than flagellum (Figs. 124-125); MD with apical tooth longer than width of inner teeth, SSd and Si present (Fig. 126): M with 2 narrowly separated, weakly peaked, median teeth and 5 pairs of lateral teeth (Fig. 127); VmP somewhat angular at posterior medial angle, but not truncate, no beard and no plate with long setae as described for *P. downesi* (Steffan 1965) (Fig. 127); 2 eyespots, 1 small and circular, the other, anterior and small (Fig. 128); maxilla as in Fig. 129; thorax and abdomen yellow with some reddish-brown pigment; AP partially fused and with a dense crown of claws of many types; PP with simple claws; thorax and abdomen with most setae very short and spine-like, the "macrochaetae" of Steffan (1965) (Fig. 130); Pc small with 5 setae; TA short and blunt.

SPECIMENS EXAMINED. NP8: 2La [COF], 1 male, 1 female LEx P [COF], alt. 1530 m.

Orthocladius (Eudactylocladius) sp.

A single larva assignable to the subgenus *Eudactylocladius* was present in the material. Unfortunately, the specimen is in poor condition, but appears to fit *O. fuscimanus* Kieffer as redescribed by Cranston (1984). The ventral surface of the head, from the PO to the base of the M is distinctly marked with dense, fine, pale spots. I have seen this character in associated larvae of a *Eudactylocladius* species from the western Nearctic. Gut contents - mixed detritus and small diatoms.

SPECIMEN EXAMINED. NP134: 1La, alt. 3500 m.

Orthocladius (Euorthocladius) poss. rivulorum gr. sp.

Two larvae from NP42 are placed in this species. Both larvae are in poor condition and cannot be fully described. Gut contents - large diatoms.

Larva. About 4.5mm in length (4th instar?); head reddish-orange, M and PM darkest; PO black; S.I bifid, spines of PE subequal and narrow; Pm simple; antenna with 5 segments, LO small, Bl slightly shorter than flagellum (Figs. 139-140); MD with short apical and 3 inner teeth, SSd and Si present; M with at least 8 lateral teeth, arrangement of median teeth uncertain, VmP weak and narrow (Fig. 141), beard may be very weakly developed (3-4 short hairs appear to arise from the surface of one VmP); thorax very darkly pigmented, abdomen darkly pigmented (dark violet-gray); abdominal setae small, postero-lateral setae of abdominal segments about 1/5 the segment length; Pc about as long as wide, setae missing.

SPECIMENS EXAMINED NP42: 2La (IV?), alt. 2520 m.

Orthocladius (Euorthocladius) sp. 1

Two larvae, both in poor condition, are assigned to this taxon even though the dark brown head of the 4th instar larva would result in it keying to *Eudactylocladius* in Soponis (1977) and Cranston et al (1983). In all other characters both larvae appear to be a typical *Euorthocladius* (Type I of Soponis 1977). A feature of possible diagnostic value is the unusually small Pc which is wider than it is high. Gut contents - detritus, small diatoms and inorganic particles.

SPECIMENS EXAMINED NP38: 1La (III), alt. 2520 m; NP150: 1La, alt. 2470 m.

Orthocladius (Euorthocladius) sp. 2

The two larvae placed in this species were collected from streams differing by almost 1500 m in elevation. The larvae will key to Type I of Soponis (1977). Gut contents - very fine detritus and very small diatoms.

Larva. About 4mm in length (4th instar?); head pale brown, PO dark laterally, much paler in section posterior of M; antenna with 5 segments, LO robust, Bl about equal to flagellum (Figs. 142-143); PE covered in both specimens by very broad Pm; MD with a short apical tooth and 4 inner teeth, SSd present (Fig. 144), Si absent?; M with 1 median and 6 pairs of lateral teeth, VmP absent or very weak (Fig. 145); thoracic segments and anterior abdominal segments with most setae (thorax) or a few setae (abdomen) short and spine-like (Fig. 146); abdomen yellowish-grey with a few long streaks of violet; claws of PP large and dark brown; Pc about as long as wide.

SPECIMENS EXAMINED. NP38: 1La (III), alt. 2520m; NP89: 1La, alt. 3995m.

Orthocladius cf. frigidus (Zetterstedt)

Chironomus frigidus Zetterstedt 1840: col. 812

Two 3rd instar larvae, one larval exuviae associated with a female pupa and one female pupal exuviae are placed in this taxon. The larval and pupal material fit the description of *O. frigidus* by Zavřel (1938) very closely and are also very similar to a common undescribed Nearctic species which is possibly *O. frigidus* as well. The

AM and lateral setae of A.VIII of the pupal exuviae are larger than those of the pupa. This is most likely individual variation, but the presence of a second species cannot be ruled out. Gut contents - fine detritus.

SPECIMENS EXAMINED NP5: 1La (III), alt. 1046 m; NP7: 1La (III), alt. 1530 m; NP28-1LEx- female P, alt. 2250 m; NP37: 1 female PEx, alt. 2480 m.

Orthocladius (O.) cf. **saxicola** (Kieffer)

Orthocladius saxicola Kieffer 1911c: 181

Specimens (larvae, prepupae and a pupal exuviae) of this species were collected from the Bhurungai Khola and its tributaries. Since the published descriptions of the immatures of *O. saxicola* are not complete, it is not possible to place these specimens more precisely. At the least, they represent a very similar species and the pupa, especially, is very close to the Nearctic *O. curtiseta* Saether (Saether, 1969). Gut contents -fine detritus and small diatoms.

SPECIMENS EXAMINED. NP26: 3La (1-III, 2-IV), 1PrP, alt. 2250 m; NP33: 1PrP, alt. 2390 m; NP35: 1 female PEx, alt. 2390 m.

Orthocladius (O.) sp.

This species, which is represented by 8 larvae from 5 Stations, is very tentatively placed in the subgenus *Orthocladius*. In Soponis (1977) and Cranston et al (1983) it will key to Eudactylocladius, but I am sure that it does not belong there. In most respects it appears to be a typical *Orthocladius* s. str., but with a dark brown head, especially on the ventral surface. I have seen similar larvae from the Nearctic which are associated with pupae that are close to *Orthocladius* s. str., but possess a definite fringe on the AL and a long RO similar to that of *O. frigidus*. Gut contents - mixture of inorganic particles (especially in larvae from glacial streams) and diatoms.

Larva. About 6mm in length (4th instar); head dark reddish-brown, PO black; antenna with 5 segments, LO moderate, Bl slightly longer than flagellum (Fig 147); S.I bifid, PE with 3 narrow, subequal spines; Pm simple, brush not visible; MD typical of *Orthocladius* s. str.; M with single median and 6 pairs of lateral teeth, middle tooth less than 2 x the width of the first lateral, VmP absent?, beard absent (Fig. 148); abdomen without conspicuous setae, darkly pigmented (blue-gray); other abdominal characters as in O. s. str.

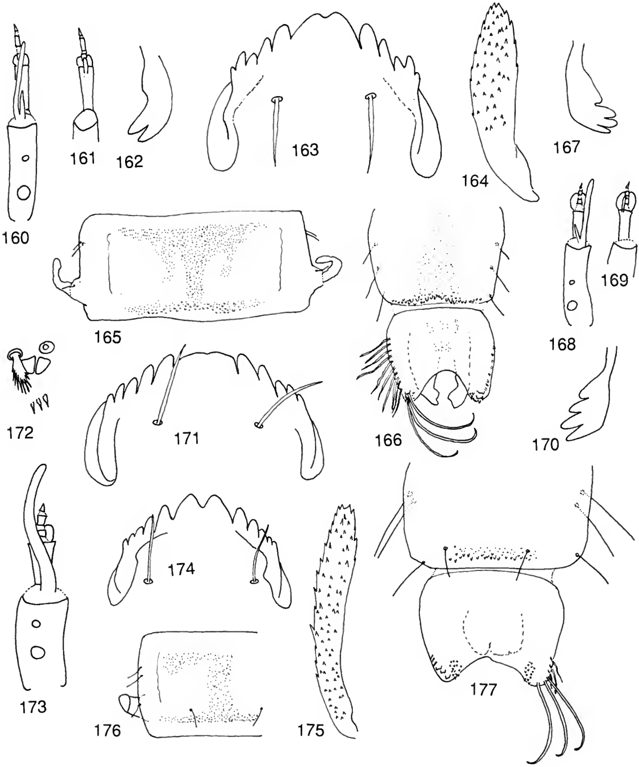
SPECIMENS EXAMINED. NP41: 2La (III), alt. 2520 m; NP72: 1La (III), alt. 3456 m; NP90: 1La, alt. 4025 m; NP98: 3La (1-III, 2-IV), alt. 4100m; NP134: 1La, alt. 3500 m.

Paracricotopus sp.

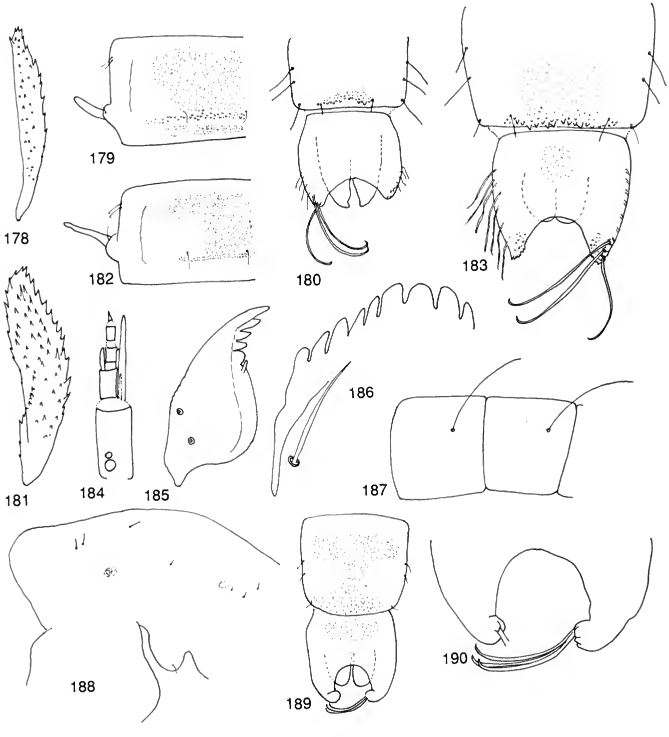
Larvae and an unassociated pupa of this species were found in collections from streams of relatively low elevation. The pupa of this species has characters not known from any described species of *Paracricotopus*, but is closest to the description of *P. niger* (Saether 1980a). The larva shows some relationship to *P. millrockensis* (Caldwell, 1985). Gut contents - small diatoms.

Pupa. Small FS on prefrons; thorax moderately rugulose; Dcs2 close to Dcs3 and Dcs4 (Fig. 157); RO large, with surface spinules and truncate at apex (Figs. 158-159); abdomen differs from *P. niger* in the following characters: (a) no median spine groups on A.II or A.III.; (b) median spine groups on A.IV-V with 22-23 large spines which are confined to the middle third of the tergite; (c) only a few median spines in group on A.VI.; (d) conjunctives A.III/IV to A.V/VI with no more than 2 rows of small spines; (e) AL with about 6 weak lateral setae; (f) most anterior AM distinctly weaker than other AM.

Larva. About 4mm in length (4th instar); head yellow-orange, PO, MD and M dark brown; antenna with 5 segments, LO moderately large, Bl to apex of 4th segment, knob at apex of ABl (Figs. 149-151); S.I bifid at apex, other labral characters apparently as typical of genus (Fig. 152); Pm simple with a relatively narrow apical tooth and an associated serrate lamella as in *P. millrockensis* Caldwell (Fig. 153); MD very



FIGS.160-177. 160-166, *Parametriocnemus* sp.1: 160, antenna with Bl; 161, flagellum of antenna without Bl; 162, Pm; 163, M; 164, RO; 165, tergum A.II; 166, tergum A.VIII and AL; 167, *Parametriconemus* sp. 2: 167, Pm. 168-171, *Parametriocnemus* sp. 3: 168, antenna with Bl; 169. flagellum of antenna without Bl; 170, Pm; 171, M. 172-177, *Parametriconemus* sp. 4: 172, labral setae, LL and PE; 173, antenna; 174, M; 175, RO; 176, tergum A.II; 177, tergum A.VIII and AL.



FIGS. 178-190. 178-180, *Parametricnemus* sp. A: 178, RO; 179, tergum A.II; 180, tergum A.VII and AL. 181-183, *Parametriocnemus* sp. B: 181, RO; 182, tergum A.II; 183, tergum A.VIII and AL. 184-187, poss. *Paratrichocladius* sp.: 184, antenna; 185, MD; 186, M; 187, A.V-VI, lateral. 188-190, *Parorthocladius* sp.: 188, distribution of thoracic setae; 189, tergum A.VIII and AL: 190, tips of AL.

similar to that of *P. niger* and *P. glaber* (Saether 1980a); M with a single, peaked median tooth and 5 pairs of lateral teeth, VmP and beard absent (Fig. 154); maxilla with PG well-developed; abdomen yellow-orange; thorax, especially of prepupa, with dark markings; abdomen with 1 long lateral seta on each side of each segment (1/2 to 2/3 length of segment); Pc with 3 strong and 2 very weak setae, as in *P. niger* (Figs. 155-156).

SPECIMENS EXAMINED. NP7: 11La (2 II, 1 III, 9 IV), alt. 1530 m; NP8: 1 male P [COF], alt. 1530 m; NP14: 3La, alt. 1548 m.

Parametriocnemus sp.1

This species was found in collections from 14 stations ranging in elevation from 1200 m to 3455 m. The larva and pupa are associated. The larva is a typical *Parametriocnemus* and appears to be very similar to *P. stylatus* (Kieffer)(RO) and *P. stylatus adzharicus* Kownacki and Zosidze (1973) (fringe on AL). Gut contents - detritus and diatoms.

Pupa. Length about 4mm; integument yellowish-brown; RO large and broad (Fig. 164); thorax moderately rugulose; Dcs1-2 close together; pearl rows well-developed; PSB on II typical for genus (Fig. 165); dorsal shagreen: A.I absent; A.II with an anterior band connected to posterior band by a longitudinal extension of the anterior band (Fig. 165); A.III-VII with uniform shagreen on surface, relatively sparse on A.VII and A.VIII; posterior band on A.III consisting of 5-6 rows of small spines, but spines are larger than shagreen spinules; posterior band on A.IV-VIII with decreasing number of rows, but size of spines increases (Fig. 166); ventral shagreen: A.II-VIII with sparse to relatively dense shagreen; A.IV-VIII (male) with posterior rows of spines, similar to those on terga; AL with weak fringe, small terminal spines and 3 large AM (Fig. 166).

Larva. About 6mm in length (4th instar); antenna with 5 segments, LO moderate, Bl to middle of 4th segment (Figs. 160-161); Pm with 2 apical teeth (Fig. 162); M with a pair of broad median teeth and 5 pairs of lateral teeth, 4th lateral distinctly taller than 3rd or 5th (Fig. 163).

SPECIMENS EXAMINED. NP14: La, alt. 1548m NP16: 1La, alt. 1610 m; NP19: 1La, alt. 2000m NP24: 1La, alt. 2135 m; NP25: 1La (III), alt. 2180 m; NP26: 20La (1-II, 2-III, 17-IV) 1 PrP, 1 male LEx P, 2 male P), alt. 2250 m; NP32: 1La (III), alt. 2390 m; NP38: 12La (10-II, 2-III), alt. 2520 m; NP 39: 2La, alt. 2520 m; NP40: 1La, alt. 2520 m; NP 43: 3La (2-III, 1-IV), alt. 2520 m NP73: 1La, alt. 3455m; NP144: 1La (II), alt. 2300 m NP152: 1La, alt. 1200 m.

Parametriocnemus sp. 2

A single larva is assigned to this species. It was collected at NP26 where *P.* sp. 1 was most abundant. Since it differs from *P.* sp. 1 only in the number of teeth on the Pm (Fig. 167), it is possible that it represents a variant of that species. However, since otherwise similar species of *Parametriocnmeus* are known to differ in the number of teeth on the Pm, it is perhaps best to separate this specimen from *P.* sp. 1. Gut contents - detritus and diatoms.

SPECIMEN EXAMINED. NP26: 1La, alt. 2250 m.

Parametriocnemus sp. 3

Seven larvae of this species were found. All but one of these were taken from streams at high elevations (above 3900m). This species may be differentiated from *P.* spp. 1 and 2 by the presence of 4 distinct teeth on the Pm (Fig. 170), the unusual proportions of segments of the antenna (Figs 168-167), the extremely large LO (Figs. 168-169) and the M which has the 4th lateral of normal length (Fig. 171).

SPECIMENS EXAMINED. NP51: 1La, alt. 2675 m; NP85: 2La, alt. 3900 m; NP90: 1La, alt. 4025 m; NP98: 1La, alt. 4100 m; NP102?: 1La, alt. 4240 m; NP120: 1La, alt. 4975 m.

Parametriocnemus sp. 4

A prepupa and a pupal exuviae of this species were collected at NP51. The larva differs from all known *Parametriocnemus* species in having the Bl much longer than the flagellum of the antenna. The pupa is basically a typical *Parametriocnemus*, but PSB on II are not as long and tapering as is typical of the genus. Gut contents - empty.

Pupa. Length about 3.5mm; integument nearly transparent; RO relatively narrow and long (Fig. 175); thorax weakly rugulose; Dcs1-2 close together; pearl rows well-developed; PSB on II well- developed, but not as narrow and pointed as usual (Fig. 176); dorsal shagreen: weak, but extensive, on all terga (Fig. 176); dorsal spine groups: posterior margin of A.II-VII with rows of spines, slightly larger on A.VI-VIII, but weak on all (Figs. 176- 177); ventral spine groups: A.VI-VII with posterior rows of weak spines, similar to those on terga; A.VIII of female with typical triangular lobes on posterior margin; AL with only a few lateral setae (Fig. 177); AL with small terminal spines and 3 AM (Fig. 177).

Larva. About 5mm in length (4th instar); head orange-yellow, PO pale, MD and M darker; S.I plumose, LL present (Fig. 172), other labral setae and chaetae simple; spines of PE small and subequal (Fig. 172); Pm not visible; antenna with 5 segments, LO large, Bl longer than flagellum (Fig. 173); tips of MD broken, apparently with apical tooth shorter than width of the 3-4 inner teeth, SSd and Si not visible, but probably present; M with a large pair of median teeth and 5 pairs of lateral teeth, VmP present (Fig. 174); maxilla not visible; abdomen orange-yellow, setae all small; Pc with 5 relatively short setae; TA short and broad.

SPECIMENS EXAMINED. NP51: 1PrP, 1 female P, alt. 2675 m.

Parametriocnemus sp. A

Three pupal exuviae of this species were found in collections from 2 stations on the same stream. No larvae of *Parametriocnemus* were found at these stations.

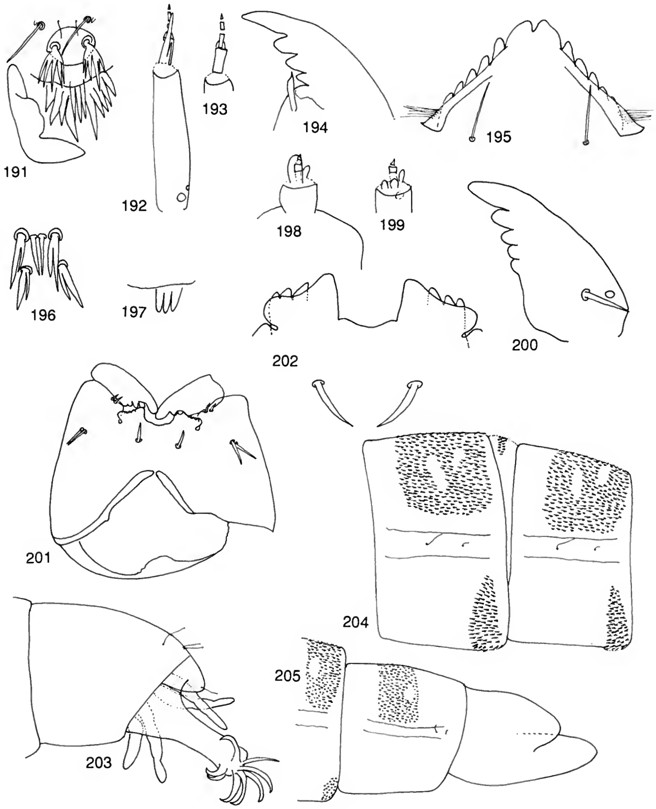
Pupa. Length about 4mm; integument yellowish-brown; RO relatively short and narrow (Fig. 178); thorax moderately rugulose along anterior dorsal margin; Dcs1-2 close together; pearl rows well-developed, mostly in 1 row; PSB on II normal (Fig. 179); dorsal shagreen: A.I with weak but extensive spinules; A.II-V with moderately strong shagreen spinules (Fig. 179); A.VI-VIII with weak shagreen development; dorsal spine groups; posterior rows of spines on A.II-VIII, weakest on A.II where there are 2-3 rows (Fig. 179), somewhat stronger on other terga (Fig. 180); ventral spine groups: A.IV-VIII (male) with posterior rows of spines similar to those of terga; AL with a few lateral setae in the distal half (Fig 180); AL with distinct terminal spinules and 3 AM (Fig. 180).

SPECIMENS EXAMINED. NP40: 1 female PEx, alt. 2520 m; NP44: 2 male PEx, alt. 2660 m.

Parametriocnemus sp. B

The pupal exuviae of this distinctive taxon was collected from one site at very low elevation (NP 8). No other *Parametriocnemus* specimens were collected at this station. It may be distinguished from the other *Parametriocnemus* pupal exuviae in the Nepalese material by the large size of the RO, the brown integument, the relatively strong development of the fringe on the AL and the strong posterior spines on the terga.

Pupa. Length about 3.5mm; integument brown, including AL; RO very large with strong lateral spines (Fig. 181); thorax moderately rugulose; Dcs1-2 close together; pearl rows well-developed - almost appear as serrations along the distal margin of the wing sheath; PSB on II normal (Fig. 182); dorsal shagreen: A.I very weak; A.II-VIII weak, but dense (Fig. 182); dorsal spine groups: posterior spines on A.II all small, in 3-4 rows (Fig. 182): A.III-VIII with larger spines and diminishing to only 1 row on A.VIII (Fig. 183); ventral spine groups: A.IV-VII (female) with posterior rows of spines;



FIGS. 191-205. 191-195, *Psectrocladius* (*P.*) *sordidellus* gr. sp.: 191, labral setae, PE and Pm; 192, antenna with Bl; 193, flagellum of antenna without Bl; 194, apex of MD; 195, M. 196-205, *Pseudosmittia* sp.: 196, labral setae; 197, PE; 198, antenna with Bl; 199b, antenna without Bl; 200, MD; 201, ventral view of head; 202, M; 203, anal segments of larva, lateral; 204, A.V-VI, lateral; 205, A.VII-VIII and AL, lateral.

A.VIII with shagreen patches lateral to the 2 triangular lobes on the posterior margin; AL with about 7 strong (for *Parametriocnemus*) fringe setae (Fig. 183); AL with distinct terminal spines and 3 AM (Fig. 183).

SPECIMEN EXAMINED. NP8: 1 female PEx [COF], alt. 1530 m.

Poss. **Paratrichocladius** sp.

A single larva (3rd instar?) of this species was found. It does not fit *Paratrichocladius* very well, e.g. the moderately dark brown head, but it fits *Cricotopus* and *Orthocladius*, the 2 other possible genera even less well. Some undescribed Nearctic larvae of *O*. (*Euorthocladius*) have long lateral setae on the abdomen. Gut contents - detritus and diatoms.

Larva. 3mm in length; head moderately dark brown; PO darker than ground color of head; antenna with 5 segments, LO slender, BL slightly less than length of flagellum (Fig. 184); S.I bifid, PE not visible, Pm bifid; MD uniformly dark, SSd present but Si may be absent (Fig. 185); M with narrow median tooth and 6 pairs of lateral teeth (Fig. 186); A.I-VII with a single, strong lateral seta which is slightly longer than the segment (Fig. 187).

SPECIMEN EXAMINED. NP 89: 1La (III?), alt. 3995 m.

Parorthocladius sp.

Six larvae from NP150 and one pupa from NP69 are placed in this taxon. Both stations are tributaries of the Marsyandi. The larvae fit the diagnosis of *Parorthocladius* in Cranston et al (1983). The pupa is close to *Parorthocladius* sp. in Langton (1984) and is very similar to a *Parorthocladius* sp. from the western Nearctic.

Pupa. length about 3mm; FS not visible, if present; RO apparently absent; thoracic chaetotaxy as in Fig. 188 (the same pattern as in the common western Nearctic sp.); wing sheaths without lateral notch; dorsal shagreen: A.I without; A.II with a weak, but broad, anterior band; A.III-VIII with a broad anterior band medially connected to a broad posterior band (Fig. 189), shagreen most extensive on A.IV and A.V; ventral shagreen not visible; all abdominal setae small, 3-4 weak lateral setae on A.VIII (Fig. 189); AL with tips turned inwards with 3 strong AM (Figs. 189-190).

SPECIMENS EXAMINED. NP69: 1 female P, alt. 3392 m; NP150: 6La (3-III, 3-IV), alt. 2470 m.

Psectrocladius (P.) sordidellus gr. sp.

Larvae of this lentic species were found only at NP 55. Gut contents - diatoms.

Larva. About 3.5mm (4th instar?); head pale yellow, PO also pale; teeth of M and MD dark; S.I palmate, Pm simple (Fig. 191); antenna with 5 segments, LO small, BL to apex of 4th segment (Figs. 192-193); MD with SSd and Si (Fig. 194); M with a pair of large median teeth and 5 pairs of lateral teeth, VmP distinct, beard present (Fig. 195); maxilla as in Fig. 9.62 of Cranston et al (1983); PC with 5 strong and 2 weak setae.

SPECIMENS EXAMINED NP 55: 16La (3, II, 12 III, 12 IV), alt. 2830 m.

Pseudosmittia sp.

Ten larvae and a pupal exuviae are assigned to this species. All of the specimens are from stations on Kali Gandaki or its tributaries. This is an unusual *Pseudosmittia* species in both stages. The association of the pupal exuviae (NP 40) with the larvae (NP 54) is by inference and may not be correct. But, given that these are the only *Pseudosmittia* specimens in the Nepalese material, that they are all from the same stream system, and that both are unusual, it seems reasonable to assume that they may be associated. The larva is a typical *Pseudosmittia* species in most respects. However, the MD and M represent an extreme development away from the typical form for the genus. The pupal exuviae is atypical in the presence of welt-like patches of anteriorly directed spines on the posterior margins of sterna A.IV-VII. Gut contents - mostly empty, but small amounts of inorganic material and diatoms in some larvae.

Pupa. FS apparently absent; RO absent; all thoracic setae small, some very short and spinule-like; 2 MAps, 3 Pcs—2 short and hair-like, 1 very short and spinule-like; 4 Dcs— Dcs 1 anterior of Dcs 2-4 which are close together; dorsal shagreen: A.I without; A.II-VIII with most of surface covered with dense shagreen (Figs. 204-205); conjunctives A.II/III-A.V/VI with a small median group of anteriorly directed spinules, those on conjunctive II/III in a row of 7-8 spinules, appearing as a row of Hl; ventral shagreen: A.IV-VII with posterior band of dense, strong, anteriorly directed spinules, much weaker group on A.VII (Figs. 204-205); no conjunctive groups on sterna; AL without AM (Fig. 205); genital sheaths of male long (Fig. 205).

Larva. Length about 4.5 mm (4th instar?); head, including PO, yellow orange; MD and M dark brown to black; S.I and S.II bifid (Fig 196), spines of PE narrow and subequal (Fig. 197); Pm simple with small, but distinct, brush; antenna with 3 or 4 segments, probably 3, very short, Bl about equal to flagellum, LO weak but evident (Figs. 198-199); MD with all teeth very large, apical tooth long and broad, apparently fits into median cavity of M, 3 lateral teeth of MD also large, occupying most of inner margin, SSd and Si absent (Figs. 200-201); M a heavily sclerotized bar with lateral and antero-lateral rounded projections and a median depressed area devoid of teeth (Figs. 201-202), M with 3 pairs of lateral teeth, beneath sclerotized bar (Figs. 202), lateral teeth probably represent the true M, the bar with processes may represent the Vm; all setae of head short and broad along most of length (Figs. 200-202); abdomen greenish- yellow, setae all weak; AP normal for *Pseudosmittia*; PP absent (Fig. 203).

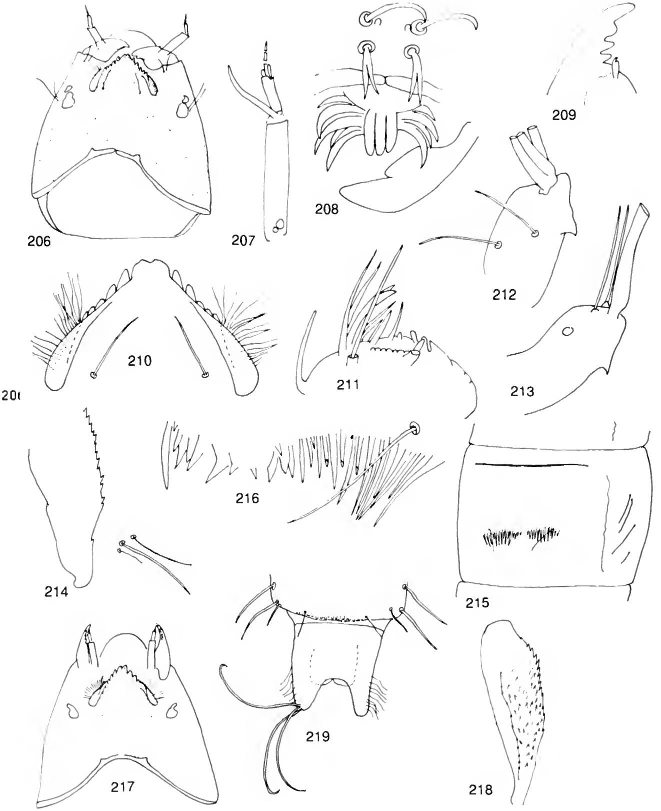
SPECIMENS EXAMINED. NP40: 1 PEx, alt. 2520 m; NP54: 7La (1-II, 6-IV?), 3La-IV [COF], alt. 2600 m.

Rheocricotopus (Psilocricotpus) sp.1

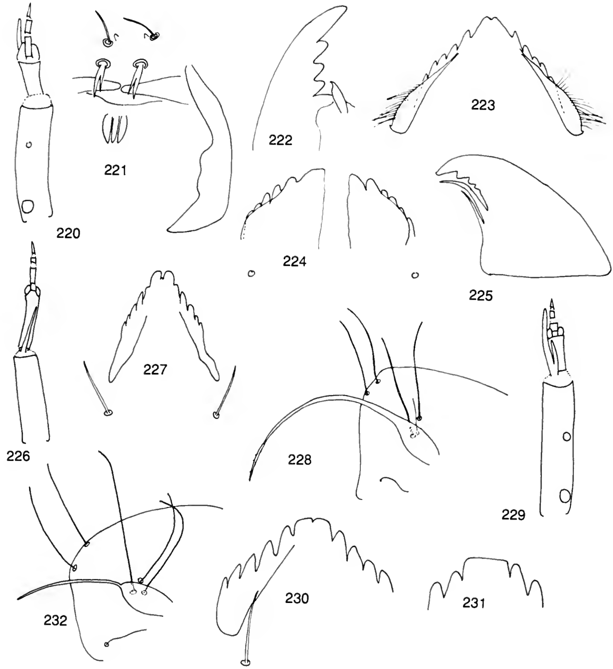
Larvae and prepupae of this species were found. The absence on the pupa of median patches of spinules on the tergites appears to place this species in the subgenus *Psilocricotopus* Saether (1985). However, further identification using the key in Saether (1985) is not possible since it is not clear if PSB is present on segment II. The larvae key most closely to *R.* (*Psilocricotopus*) *atripes* (Kieffer) in Saether, 1985. The larva of this species may be separated from *Rheocricotopus* (*Psilocricotopus*) sp. 2 by the pattern of pigment on the head. Gut contents - detritus, sometimes coarse, and diatoms.

Pupa. The pupal structures have been determined from two prepupae, neither of which is very mature. RO broad and with well-developed lateral spines (apex could not be seen) (Fig. 214); Pcs of very unequal sizes (Fig. 214); A.II-VI? with 3 strong lateral setae, the 2 anterior setae close together (Fig. 215); PSB not visible on segment II, but may be present; A.VII with 4 lamellar LS and A.VIII with 5; no dorsal or ventral shagreen evident; dorsal spine groups: A.II with a dense posterior group of Hl; A.III-VI with posterior band of very long spines which continues along the posterior margin but is weakest in the median area (Figs. 215 -216); ventral spine groups: A.IV-VI with posterior spine band as on terga, a much weaker group of posterior spines on A.VII: AL with 3 long, strong AM; fringe setae not visible, if present.

Larva. Length about 5mm (4th instar); head patterned in yellow and reddish-brown, PO dark and narrow (Fig. 206); antenna with 5 segments, LO moderate in size, Bl slightly less than length of flagellum (Fig. 207) S.I deeply divided, S.II strong and simple; Pm simple, spines of PE narrow and subequal (Fig. 208); MD with SSd (hooked at terminus) and Si present (Fig. 209); M with a pair of broad median teeth, VmP large, strong beard present (Fig. 210); maxilla with PG well-developed (Fig. 211); thorax of 4th instar and prepupa patterned with orange-red pigment; abdomen yellow to yellow-orange; thoracic and



FIGS. 206-219. 206-216, *Rheocricotopus (Psilocricotopus)* sp.1: 206, head, ventral; 207, antenna; 208, labral setae, PE and Pm; 209, apex of MD; 210, M; 211, maxilla; 212, Pc with strong setae; 213, Pc with two strong setae removed; 214, RO and Pcs. 215, A.VI, dorsal; 216, posterior spine groups of A.VI, dorsal. 217-219, *Rheocricotopus (Psilocricotopus)* sp. 2: 217, head, ventral view; 218, RO; 219, posterior margin of A.VIII and AL, dorsal.



FIGS. 220-232. 220-223, *Rheocricotopus (Rheocricotopus)* sp.: 220, antenna; 221, labral seta, PE and Pm; 222, MD; 223, M; 224, *Smittia* sp.: 224, M; 225, *Synorthocladius* cf. *semivirens*: 225, MD. 226-227, poss. *Thienemanniella* sp.: 226, antenna; 227, M; 228, *Tvetenia bavarica* gr. sp.: 228, RO and anterior thorax. 229-232, *Tvetenia discoloripes* gr. sp.: 229, antenna; 230, M; 231, M with worn median teeth; 232, RO and anterior thorax.

abdominal setae moderately long (1/5-1/4 segment length); PC with strong spur and 3 large and 2 very small setae (Figs. 212-213).

SPECIMENS EXAMINED. NP12; 1La, alt. 1462 m; NP14: 6La, 1 PrP, alt. 1548 m; NP16: 2La, alt. 1610 m; NP18: 7La (2-III, 5-IV), alt. 2000 m; NP19: 1La , alt., 2000 m; NP26: 2La, 1 PrP, alt. 2250 m; NP38: 1La, alt. 2520 m.

Rheocricotopus (Psilocricotopus) sp. 2

The larva of this species is very similar to that of *R.* (*Psilocricotopus*) sp. 1. differing only in the patterning of the ventral side of the head. The pupa assigned to this taxon is a typical *Psilocricotopus*, but is not directly associated with larvae. It is very close to *R.* (*Psilocricotopus*) *tirolus* Lehmann (Saether 1985). All of the pupae were taken at NP 26, where most of the larvae assigned here were found. Since the larva of *Psilocricotopus* sp. 1 is associated directly with the unusual pupa, it seems reasonable to assume that the second type of *Psilocricotopus* larva found at NP 26 belongs with the typical pupa of *Psilocricotopus* sp. 2. Gut contents - detritus and diatoms.

Pupa. RO very broad (Fig. 218); Pc of different sizes as in *Psilocricotopus* sp. 1; abdominal characters typical of *Psilocricotopus*, PSB absent on segment II; AL with 3 AM and a very weak fringe (Fig. 219).

Larva. About 5mm in length; head patterned in yellow and brown (Fig. 217); all other characters as in *R.* (*Psilocricotopus*) sp. 1.

SPECIMENS EXAMINED. NP14: 1LA (3-II, 8-III), alt. 1548 m; NP18: 5La (III), alt. 2000m NP 22-1La (III), alt. 2000 m NP26: 1LA , 3 female P, alt. 2250 m; NP37: 1LA, alt. 2480 m; NP39: 1LA, alt. 2520 m.

Rheocricotopus(Rheocricotopus) sp.

The larvae placed in this taxon have subequal spines of the PE, small abdominal setae, a strong spur on the Pc and 5 subequal setae on the Pc. All of these are characters associated with the subgenus *Rheocricotopus*. The pupa, which is not associated, but from the station where most of the larvae were found, is a typical *fuscipes* group pupa. Gut contents - coarse to moderate sized detrital particles and diatoms.

Pupa. The pupa keys to and agrees with the description of *R. effusus* (Walker) in Langton (1984), Lehmann (1969) and Saether (1985).

Larva. Length about 5mm; head yellow; M, MD and Pm brown; PO yellow to brown; antenna with 5 segments, LO large, Bl reaching apex of 3rd segment (Fig. 220); S.I deeply bifid, S.II simple and much weaker than in *Psilocricotopus*, scales of PE subequal, Pm simple (Fig. 221); MD as in Fig. 222; M with paired median teeth and 5 pairs of lateral teeth, VmP large, beard well-developed (Fig. 223); maxilla with PG much more weakly developed than in *Psilocricotopus* group; abdomen reddish-orange, thorax patterned with reddish-brown; abdominal setae small; Pc with sharp spur and 5 subequal setae.

SPECIMENS EXAMINED. NP8: 1La, alt. 1530 m; NP14: 3La, alt. 1548 m; NP26: 21La (9-III, 12-IV), 1 female P, alt. 2250 m; NP83: 1La, alt. 3770 m; NP102: 1La, alt. 4240 m.

Smittia sp.

A single larva, in very bad condition, is assigned to this taxon. Most of the important diagnostic features are not visible. The M has a broad median tooth and 5 pairs of lateral teeth (Fig. 224); the Pm is bifid; AP with numerous basal spinules and a few terminal claws (fig. 9.68 in Cranston et al 1983); PP much reduced (absent?) with claws distributed as in *S. aquatilus*. Gut contents - empty.

SPECIMEN EXAMINED. NP150: 1La (IV?), alt. 2470 m.

Symposiocladius cf. lignicola (Kieffer)

Orthocladius lignicola Kieffer in Potthast 1915: 273
Symposiocladius lignicola Cranston 1982b: 421

A larva of this species was found in material from NP38. It differs from the description of *S.*

lignicola (Cranston, 1982b) only in the absence of inner serrations on the claws of the AP and in the absence of setal tufts on the abdomen. Since this specimen is an early instar (probably 2nd), the significance of the absence of these structures is questionable. Gut contents - small detrital particles and diatoms.

SPECIMEN EXAMINED. NP38: 1La (II?), alt. 2520 m.

Synorthocladius cf. **semivirens** (Kieffer)

Dactylocladius semivirens Kieffer 1909: 48

Two larvae of this species were found. The only difference between these larvae and the description of *S. semivirens* is the unusual development of the SSd and serration of the inner margin of the MD. Both of these are long in *S. semivirens*, but in these specimens they are exceptionally long (Fig. 225). The SSd extends almost to the tip of the MD and the serration is about 2/3 as long. The distance between the basal tooth of the MD and SSd is unusually great (Fig. 225). Gut contents - fine detritus and diatoms.

SPECIMENS EXAMINED. NP26: 1La, alt. 2250 m NP38: 1La, alt. 2520 m.

Thienemanniella acuticornis (Kieffer)

Corynoneura acuticornis Kieffer 1912:101

Larvae, prepupa and a pupa of *T. acuticornis* were collected. Both the larva and pupa agree with the published description of *T. acuticornis* in all details. Gut contents - fine detritus and small diatoms.

SPECIMENS EXAMINED. NP12: 1La, alt. 1462 m; NP14: 2La (1 II, 1 IV), alt. 1548 m; NP16: 2La, 1 female P, alt. 1610 m; NP26: 2La, 1 PrP, alt. 2250 m; NP33: 1La, alt. 2390 m; NP38: 2La, alt. 2520 m; NP51: 1La, alt. 2675 m.

Thienemanniella cf. **clavicronis** (Kieffer)*

Thienemanniella clavicronis Kieffer 1911d: 201

A single specimen of this species with a dark brown head was found in material from NP 19. It fits the description of *T. clavicornis* in Cranston (1982a) and keys to *Thienemanniella* sp. B in Thienemann (1941). The larval body is violet in color. Gut contents - fine detritus and small diatoms.

SPECIMEN EXAMINED. NP 19: 1La, 2000 m.

Thienemanniella sp. 1

Larvae of this species were found at 3 sites. It is a typical *Thienemanniella* and keys to species B in Cranston (1982a). Gut contents - fine organic detritus and diatoms.

SPECIMENS EXAMINED. NP26: 7La, alt. 2250 m; NP38: 2La (1-III, 1-IV), alt. 2520 m; NP150: 1La, alt. 2470 m.

Poss. **Thienemanniella** sp.

A single larva of this unusual species was found at NP 5. If it is a *Thienemanniella* species, it represents a new form of that genus. It is also possible that it belongs in *Eukiefferiella*, but if it does, it would be a new form of that genus as well. Gut contents - small diatoms.

Larva. About 1mm in length (2nd or 3rd instar?); head uniformly pale brown, PO darker; antenna with 5 uniformly pale brown segments, LO small, but distinct, Bl less than length of the 2nd segment (Fig. 226); labrum not visible; MD apparently normal; M with a pair of prominent median teeth, with a tiny tooth between, and 5 pairs of lateral teeth, the first laterals appressed to medians (Fig.s 227); abdomen plump without obvious setae; salivary glands distinct; PP short possibly without ventral seta.

SPECIMENS EXAMINED. NP 5: 1La (II or III?), alt. 1046 m.

---

*Most authors cite this species as *T. clavicornis* but in the original paper it is printed as *T. clavicronis*.

Tvetenia bavarica gr. sp.

Specimens of this species were among the most abundant orthoclads in the collections and were taken from streams ranging in elevation from 1548 m to 4100 m. Association of the larva and pupa is based on several prepupae. The larva is typical of the *bavarica* gr. and agrees in all observable structures with the Nearctic *T. paucunca* Saether. The pupa is also very close to this species and shares with it the presence of Hl only on conjunctives III/IV and IV/V. The Hl are bifid. It differs from *T. paucunca* only in the absence of weak posterior spines on the dorsal surface of A.I, in the shape of the RO (Fig. 228) and the relative size of the Pc setae (Fig. 228). A partially developed pharate male appears to have genitalia structures that are in agreement with *T. paucunca*. This species is possibly *T. altimontanus* Tokunaga (1966) which was placed in the genus *Nanocladius* (O.A.S. pers. comm.). Gut contents - mixed detritus and diatoms.

SPECIMENS EXAMINED. NP14: 1La, (III), alt. 1548 m; NP16: 2La, alt. 1610 m; NP18: 1La (III), alt. 2000 m; NP25: 1La, alt. 2180 m NP26-19La (2-II, 12-III, 5-IV), 3PrP, 1 male, 1 female P, alt. 2250 m; NP32: 2La, alt. 2390 m; NP37: 2La, 1 male PEx, alt. 2480 m; NP 38: 6La (2-II, 1-III, 3-IV), alt. 2520 m; NP 83: 4La (III), alt. 3770 m NP90: 1LA, alt. 4025 m; NP 98-1La, alt. 4100 m; NP150: 12La (1-II, 1-III, 10-IV), 2PrP, alt. 2470 m.

Tvetenia discoloripes gr. sp.

This species was collected much less frequently and over much less range in elevation that was *T. bavarica* gr. sp. Larvae of this species will key to *T. discoloripes* in Cranston (1982a) and the pupae will key to *T. verralli* in Langton (1984). Gut contents - detritus and diatoms.

Pupa. RO with unusually thin terminal filament arising from base without tapering (Fig. 232); distal margin of wing sheaths with a single row of strong denticles (pearl row); dorsal spine groups: A.I without posterior spines, A.II-VIII with a posterior row of spines, not interrupted in middle; Hl on conjunctives III/IV to V/VI (about 4 in each group), Hl not bifid at apex; ventral spine groups: A.IV with a few small posterior spines, 4-5 in lateral groups and 3-4 widely spaced between the lateral groups, A.V-VIII of male with an uninterrupted posterior row of spinules; a few very poorly developed pigment spots on some conjunctives, but probably more in mature specimens; L_1 and L_2 close together, L_2 about two-thirds length of L_1.

Larva. About 4mm in length (4th instar); head yellow, PO black, MD and M brown; antenna with 5 segments, LO moderately large, Bl about equal to flagellum (Fig. 229); S.I with distal points, almost plumose; Pm simple and distally broad; MD typical of genus and with 2 serrations on inner margin; M with a pair of median teeth and 5 pairs of lateral teeth, median teeth often reduced to a single broad tooth (Figs. 230-231); abdomen with most setae large L1 and L2 almost subequal; Pc well-developed; abdomen often with some violet pigmentation.

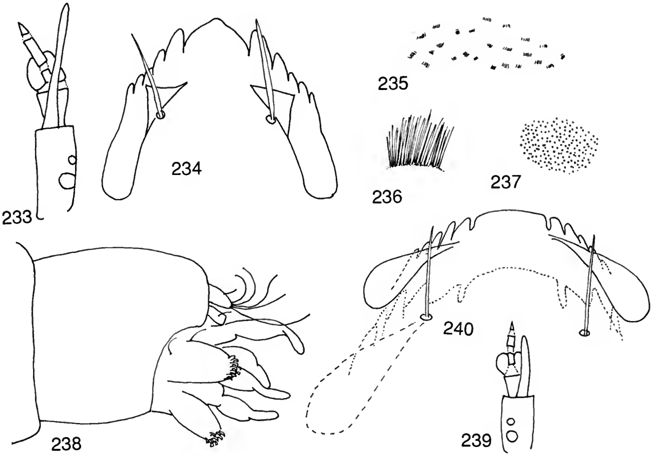
SPECIMENS EXAMINED. NP14: 4La, alt. 1548 m; NP16: 1La, 1 PrP, alt. 1610 m NP 25: 1 male, 1 female P, alt. 2180 m; NP64: 1La, alt. 3150 m; NP150: 1LA, alt. 2470 m.

Paraphaenocladius cf. **pseudirritus** Strenzke

Paraphaenocladius pseudirritus Strenzke 1950: 216

A single larva from NP 26 is placed in this taxon. Gut contents - empty.

Larva. About 3.5-4mm in length (4th instar?); head yellow, PO yellow, M and MD brown; S.I plumose, PM bifid; antenna with 5 segments, LO very large; Bl about equal to flagellum (Fig. 233); M with a peaked median tooth and 5 pairs of lateral teeth, VmP large, beard absent (Fig. 234); MD broken, but SSd and Si present, apical tooth short, 3 inner teeth; AP partially fused and with numerous claws and spines forming the crown, on the base of the AP there are tufts of minute spines (setae?) (Figs. 235-237); PC large with 3 strong and at least 2 weaker setae; PP unusually



FIGS. 233-240. 233-238, *Paraphaenocladius* cf. *pseudirritus:* 233, antenna; 234, M; 235, spine tufts on base of PA; 236, spine tuft of PA, lateral view; 237, spine tuft of AP, end view; 238, posterior segments of larva, latera.; 239-240, *Orthocladiinae* sp.1: 239, antenna; 240, M and developing mentum of next instar.

short (Figs. 238).

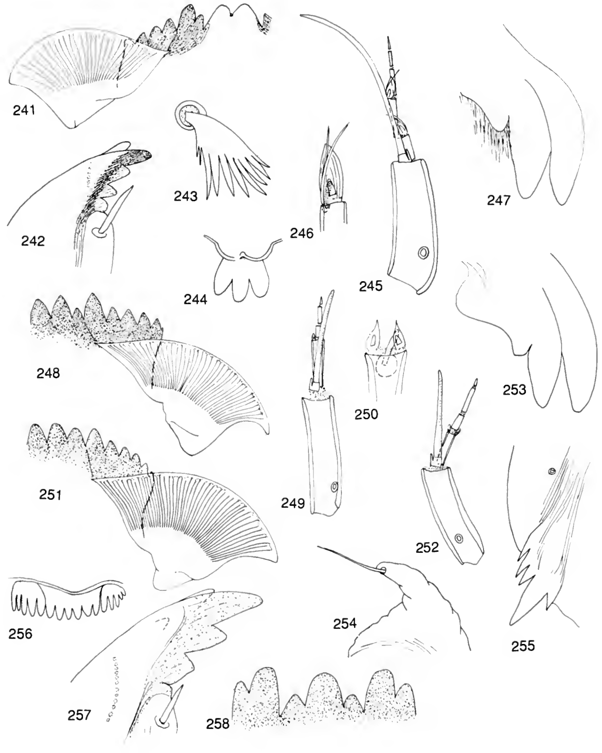
SPECIMEN EXAMINED. NP26: 1La (IV?), alt. 2250 m.

Orthocladiinae sp. 1

A larva found in the material from NP90 is placed in this species. Not all critical diagnostic features are visible and that, together with its small size (2mm) and early instar, prevents a more precise placement. Based on the M it appears to be close to *Stilocladius*, but using a combination of characters it is perhaps better placed near *Paraphaenocladius*. It appears to be very close to *Paraphaenocladius* sp. c(?) of Strenzke (1950). The developing M and VmP of the next instar indicate that the larva is no more than a third instar. Gut contents - empty.

Larva. About 2mm in length (3rd instar?); head orange-yellow; S.I bifid or multi-branched, clearly not simple; Pm probably bifid; antenna short, with 5 segments, LO extremely large, Bl about to apex of 4th segment (Figs. 239); MD with short apical and 3 inner teeth; M with a broad median tooth and 5 pairs of lateral teeth (Fig. 240); abdomen with segmental stripes of violet; orientation of PP and Pc normal, not as in *Paraphaenocladius.*

SPECIMEN EXAMINED. NP90: 1La (III?), alt. 4025 m.



FIGS. 241-258. 241-247, *Microtendipes* sp. larva. 241, VmP and M; 242, apex of MD; 243, seta SI; 244, PE; 245, antenna; 246, detail of LO; 247 apex of PrM. 248-250, *Polypedilum* sp. 1 larva: 248, VmP and M, 249. antenna; 250, detail of Bl_2 and LO. 251- 252, *Polypedilum* sp. 2 larva: 251, VmP and M; 252,antenna; 253. PrM. 254-255,*Polypedilum* sp. 3, pupa: 254, CT; 255, candolteral spur A.VII. 255-258, *Chironomus* sp. larva: 256, PE; 257, apex MD; 258, center of M.

Subfamily CHIRONOMINAE
Tribe CHIRONOMINI

The Chironomini of Nepal as represented by the material herein reported was rather sparse and different from the fauna found in Bolivia-Peru (Roback & Coffman 1983) at comparable altitudes. Only one species of *Chironomus* was found in Nepal (possibly five in Bolivia-Peru) and two or three species of *Polypedilium.* The larvae were subgenus *Polypedilium.* In Bolivia-Peru seven *Polypedilum* species were found, all subgenus *Tripodura. Microtendipes*, found in Nepal, was not present in the SA collections.

Microtendipes sp.

The single larvae of this genus found in Nepal belongs to the *pedellus* group and strongly resembles *M. caducus* Townes. A_{2-4} are in the ratio 1.0:1.3:1.0.

Larva. Head pale brown; PE simple, three broad (Fig. 244) equal teeth; PrM essentially bifid (Figs. 247), third tooth at best indistinct; brush present; S.I plumose (Figs. 243); antenna as in Fig. 245; A_1 66µ with CS, A_1 0.33 from base; A_2 15µ; A_3 20µ; A_4 15 ; A_5 10µ; A_6 7µ; A_{2-6}/A_1 1.06; LO on A_2 and A_3, 13µ L with 16µ filaments (Figs. 246); Bl 102µ; ABl 7µ; Bl_2 6µ (on A3); Bl/A_{2-6} 1.46; MD as in Figs. 242, 137µ; dorsal tooth pale; A_1/MD 0.48; M and VmP as in Fig. 241; median tooth unevenly trifid and pale (Fig. 241); M 108µ W; VmP 83µ W: VmP/M 0.77; Pc 29µ L x 22µ W; with 8 median brown apical setae and two unequal lateral setae; PP with 16 pale simple claws in "semi-horseshoe" arrangement; TA 259µ L x 33µ greatest width.

SPECIMEN EXAMINED. NP 1: 1La, alt. 1462 m.

Genus **Polypedilum** Kieffer

Polypedilum sp. 1

This is a very typical *Polypedilum* larva with the tall medians, short outer medians and tall first lateral teeth of the mentum (Fig. 248).

Larva. Head pale brown; PE with distally serrate plates; PrM unevenly trifid, similar to Fig. 253; A_1 60-63µ; CS, A_1 0.24- 0.26 from base; A_2 23-26µ; A_3 5-6m; A_4 7-10µ; A_5 4-6µ; Bl 54-58µ; A_{2-5}/A_1 0.79-0.83; Bl/A_{2-5}1.08-1.16 (Fig. 249); ABl 11µ; Bl_2 on A_2 (Fig. 250) 7µ; LO (Fig. 250) conical 5-6µ; MD 126-127µ with dorsal tooth; A_1/MD 0.48-0.50; VmP and M as in Fig. 248; VmP 99-102µ W; M 108-117µ; Vm P/M 0.87-0.92; Pc membranous, 15µ L and W, with eight apical setae and two subequal laterals; TA 138µL with constriction 0.42 from base; PP with 14 pale simple claws.

SPECIMENS EXAMINED. NP12: 13La, alt. 1462 m; NP18: 1La, alt. 200 m; NP 26: 2La, alt. 2250 m NP126: 1La, alt. 850 m..

Polypedilum sp. 2

This species with its more evenly tapering teeth of the mentum (Fig. 251) resembles *P. convictum* (Walker) as figured by Pinder & Reiss (1983).

Larva. Head pale brown; PE as in *P.* sp.1; PrM as in Fig. 253, antenna as in Fig. 254; A_1 54-55µ; CS,A_1 0.26-0.27 from base; A_2 18-20µ; A_3 8-9µ; A_4 13-15µ; A_5 4-5µ; A_{2-5}/A_1 0.98; Bl/A_{2-5} 1.00-1.02; LO as in *P.* sp.1; MD 124-134µ; A_1/MD 0.41-0.44; VmP and M as in Fig. 251; VmP 102-111µ W; M 105-111µ W; VmP/M 0.97-1.00; Pc as in *P.* sp. 1, 18µ L; TA 399µ L; with constriction 0.46 from base; PP with 13 pale simple claws.

SPECIMENS EXAMINED. NP25: 4 La, alt. 2250 m; NP37: 1 La, alt. 2480 m; NP38: 1 La (?III), alt. 2520 m; NP150: 1 La, alt. 2470 m.

Polypedilum sp. 3

This species is represented by a single pupa. The other *Polypedilum* species collected in Nepal were not found at the same station as this pupa.

Pupa. Cephalic tubercle as in Fig. 254; apical seta 100; abdomen about 5.1 mm long; row of recurved hooks on A.II with 75 hooks; anterior spinule patch of A.II-V barely heavier than mesal fenestrated area of spinules; intersegmental membranes III- IV, IV-V with transverse spine patches, not much stronger than anterior bands on tergites; vortex patches present postero- laterally on A.IV; V; LS filaments of A.V-VIII, 3-3-4-4; AL with 35-37 LS filaments, more strongly grouped toward apex; caudolateral spur A.VIII, Fig. 225.

SPECIMEN EXAMINED. NP 54: 1 female P, alt. 2600 m.

Genus Chironomus

Chironomus sp.

These larvae appears to belong to the subgenus *Chironomus*. They resembles *Chironomus* (C.) *decorus* Joh. and were found in a pool and a small reservoir.

Larva. Head pale brown; PrM bifid; PE, three toothed plates (Fig. 256); A_1 117μ; CS, A_1 0.41 from base; A_2 38μ; A_3 9μ, A_4 13μ; A_5 7μ; Bl 69μ; ABl 15μ; A_{2-5}/A_1 0.68; Bl/A_{2-5} 0 87; MD 296μ with apical tooth, two inner teeth, dark inner shoulder and pale dorsal tooth (Fig. 257); SSd simple, short (Fig. 257); A1/MD 0.40; VmP and M typical for genus; mesal teeth as in Fig. 258; VmP 178μ; M 167μ W; VmP/M 1.07; A.IX with one pair of TL; A. X with two pair of TV; Pc 32μ L x 29μW with seven pale apical setae and two unequal fine laterals.

SPECIMENS EXAMINED. NP54: 2La, alt. 2600 m; NP55: 2La, alt. 2830 m.

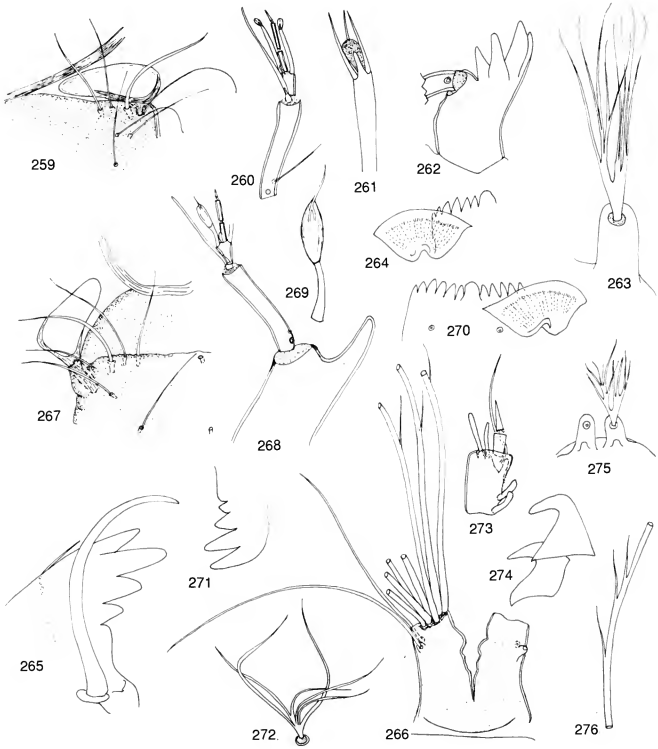
Tribe Tanytarsini

The overall tanytarsine fauna found in Nepal is quite diverse when compared to that of Bolivia-Peru. In Nepal three-four genera of the "Tanytarsariae connectentes" were present (none in Bolivia-Peru). *Tanytarsus* was present in both faunas, though only one species in each case and *Micropsectra*, the dominant genus in Nepal (11 species), was not present in Bolivia-Peru. *Paratanytarsus* was present only in Bolivia-Peru and one unknown genus, near *Tanytarsus* in Bolivia-Peru and near *Micropsectra* in Nepal, was present. The genus *Rheotanytarsus* was present in both faunas. Of the two following genera, the first would normally be placed in *Stempellina* on the basis of the palmate apicomesal projection of the antennal tubercle (Fig. 262) and the second in *Constempellina* on the basis of the simple blunt projection (Fig. 268) Both have the following characters in common: (1) T.I with apicolateral shoulder plates (Figs. 259. 267) - the function of these is unknown; (2) LO both on apex of A_2 and shorter than or subequal to A_{3-5} (Figs. 260, 268); (3) Bl slightly longer than A_{3-5}; (4) plumose S3 on tubercles (Figs. 263, 275), (see Oliver et al 1978, Fig. 97); (5) Pc membranous with unequal laterals and finely pectinate apical setae (Figs. 266, 276). Brundin (1948: fig. 17) shows a species of *Constempellina* with longer pectinations. They differ in the aforementioned structure of the antennal tubercle projection and in the structure of the lauterborn organs (Figs. 261, 269).

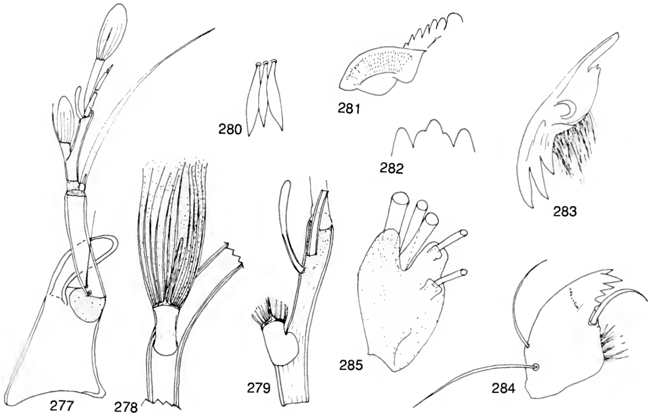
On the basis of the Pc and S3 structure these genera are placed near *Constempellina* but this is strictly a designation of convenience. The structures of these genera and the two other genera which follow suggest that when the worldwide fauna (all stages) is known the generic concepts within the "Tanytarsariae connectentes" will require considerable redefinition.

Genus 1 nr. Constempellina

Larva. Head pale brown; S3 plumose (Fig. 263) on short tubercle; tubercle 15μ, seta 34μ; PE with three separate pointed scales as in Fig. 280; Pm appears to have 3 + apical teeth and a distinct brush; antenna with two LO apically on A_2 (Fig. 260); PLO 20μ; LO with core and three filaments (Fig. 261); core 9μ, filaments 13μ; A_1 51μ; lateral seta A_1 0.20 from base; A_2 13μ; A_3 10μ; A_4 15μ; A_5 7μ; total LO length subequal to A_{3-5}; Bl 57μ; ABl 9μ; Bl_2 6μ, Bl/A_{2-5} 1.14; MD (Fig. 265) 88μ with darker apical, two lateral



FIGS. 259-276. 259-266, Genus 1 nr. *Constempellina*, larva: 259, articulated plate; 260, antenna; 261, detail of LO; 262, APe; 263, seta S3; 264, VmP and M; 265, apex of MD; 266, dorsal view of Pc and base of apical setae. 267-276, Genus 2 nr. *Constempellina*, larva: 267, articulated plate; 268, antenna and APe; 269, detail of LO; 270, VmP and M; 271, apex of Pm; 272, ventral seta T.II; 273, maxillary palpus; 274, two claws of PPl 275, seta S3; 276, detail of apical seta of Pc.



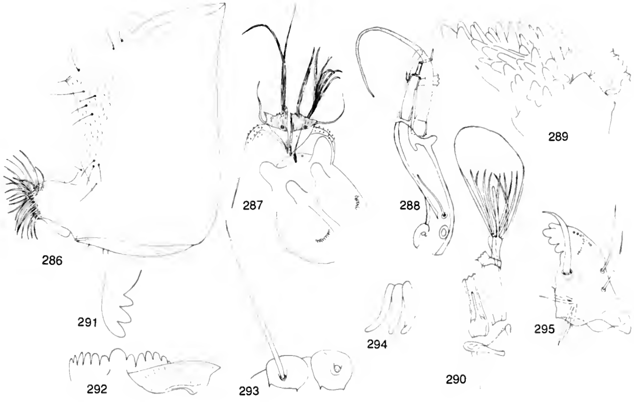
FIGS. 277-285. *Stempellinella* sp., larva: 277, antenna and APe; 278, detail of lower LO; 27,. detail of apex of A_2 and $Bl_{2:}$ 280, PE; 281, VmP and M; 282, unworn mesal tooth of M; 283, PE; 284, MD; 285, Pc with base of apical setae and LaPC.

teeth and paler dorsal tooth; A_1/MD 0.58; VmP and M as in Fig. 264; VmP 51μ; M width 64 ; apicomesal tubercle of APe with 4-5 lobes, 35 μ across apices of lobes; anterodorsal corners of T.I each with an articulated plate (Fig. 259) 133 L; dorsal setae of T.I shown in Fig. 259; Pc membranous, apically with slight sclerotization; each 66 μ L x 25 μ W; 7 apical setae, finely pectinate (Fig. 266); two unequal lateral setae; TA conical 58 μ L, 39 μ wide at base; PP with 15 simple claws at apex, arranged in "horseshoe" configuration.

SPECIMEN EXAMINED. NP38: 1La, alt. 2520 m.

Genus 2 nr. **Constempellina**

Larva. Head pale, about 250 μ L; S3 plumose (Fig. 275) on short tubercle; tubercle 15 x 9 μ; S3, 38μ; SI comb-like, bases fused; SII plumose mostly on inner side; labral lamella present; PE not clearly visible, appears similar to Fig. 280; Pm with 4 teeth and distinct brush (Fig. 271); antenna with two LO apically on A_2; PLO 10μ; main body 13μ; apical filament extends 10μ beyond apex of main body (Fig. 269); A_1 53μ; lateral seta about 0.20 from base; A_2 12μ; A_3 9m; A_4 12μ; A_5 4m; total LO length (33μ) subequal to A_{3-5}; A_{2-5} 47μ; Bl 55μ; ABl 6μ; Bl 28μ; Bl/A_{2-5} 1.19; MD, 80μ L, as in Genus 1 nr. *Constempellina*; maxillary palpus as in Fig. 273;



FIGS. 286-295. Genus nr. *Stempellina*, larva. 286, T.I and AP, lateral; 287, apex of abdomen with Pc, ventral; 288, antenna without LO; 289, APe; 290, detail of LO and ABl; 291, apex of Pm; 292, VmP and M; 293, possible S3; 294, PE; 295, MD.

VmP and M as in Fig. 270; VmP 53μ, M 63μ wide; APe with simple blunt apicomesal tubercle (Fig. 268) about 37μ L; anterodorsal corners of T.I with articulated plate (Fig. 267), 110μ L x 55μ deep at base; dorsal setae of thorax (Fig. 267) simple, some ventral setae (Fig. 272) plumose; Pc as in Fig. 266, 76μ L x 26μ W; detail of part of pectinate apical seta in Fig. 276; TA conical 66μ L x 51μ W at base; PP with 17 simple claws at apex (Fig. 274) arranged in "horseshoe" configuration.

SPECIMEN EXAMINED. NP150: 1La, alt. 2470 m.

Stempellinella sp.

On the basis of the antennal structure (Fig. 277) and the form of the PE (Fig. 280) and Pm (Fig. 283) this species falls in *Stempellinella.*

Larva. Head pale; S3 appears simple, not on tubercle; PE, three scale-like pointed lobes (Fig. 280); Pm (Fig. 283) with three teeth, weakly inclined to main axis; brush present; antenna and APe as in Fig. 277; APe with elongate rounded apicomesal tubercle, 42μ L; A$_2$ with two LO; lower LO 0.23 from base with short PLO, 9-10μ L; upper LO apical on A$_2$ with PLO 23- 26μ L; LO, 24-28μ L (Fig. 278); Bl 108μ; ABl 9μ; Bl$_2$: 19-20μ L, 0.77 from base of A$_2$ (Fig. 279); A$_1$ 60-61μ; lateral seta A$_1$ subbasal near CS,A$_1$ (Fig. 277); A$_2$ 37-41μ; A$_3$ 12-13μ (Fig. 277); A$_4$ 9-10μ; A$_5$ 4μ; Bl/A$_{2-5}$ 1.48; MD 79μ (Fig. 284) with apical tooth, 3 inner teeth and a paler dorsal; A$_1$/MD 0.76; VmP 47m W (Fig. 28); M 64μ W (Fig.s 281); mesal tooth (unworn) trifid (Fig. 282); T.I without anterodorsal plates; Pc (Fig. 285) membranous, 26μ L x 19μ W; 2-3 apical setae, no pectinations, 204μ L; two LaPc about

TABLE 2. Measurements (μ), altitude, (m) and mean of measurements, ratios, altitude for larvae of ***Rheotanytarsus***. r= range of measurements, number in [] = n for mean.

	SP 1		SP 2	
	r	mean	r	mean
APe-L	44-48	43.3 [3]	66-73	68.3 [3]
A_1-L	70-86	77.4 [5]	108-117	111.5 [6]
LS, A_1-Pos	0.55-0.68	0.616 [5]	0.53-0.63	0.593 [5]
A_2-L	18-21	19.3 [3]	22-23	22.4 [5]
TotalLO-L	16-20	17.0 [4]	19-22	20.2 [5]
B1-L	35-41	38.0 [2]	38-51	45.8 [4]
AB1-L	20-22	20.7 [3]	22-31	27.5 [4]
A_1/A_2	3.72-4.06	3.890 [2]	3.78-4.56	4.180 [6]
LO/A_{35}	0.84-0.95	0.893 [3]	0.86-0.96	0.892 [5]
B1/AB1	0.54-0.57	0.555 [2]	0.58-0.61	0.603 [4]
MD-L	85-88	86.6 [5]	101-110	105.3 [4]
A_1/MD	0.82-1.00	0.892 [5]	1.02-1.09	1.063 [4]
VmP-L	54-66	59.8 [5]	64-73	70.4 [5]
M-L	55-66	59.8 [5]	76.85	79.6 [5]
VmP/M	0.95-1.05	1.002 [5]	0.84-0.96	0.884 [5]
Altitude (m)	1046-3500	2139.2 [6]	1360-2520	2375.1 [7]

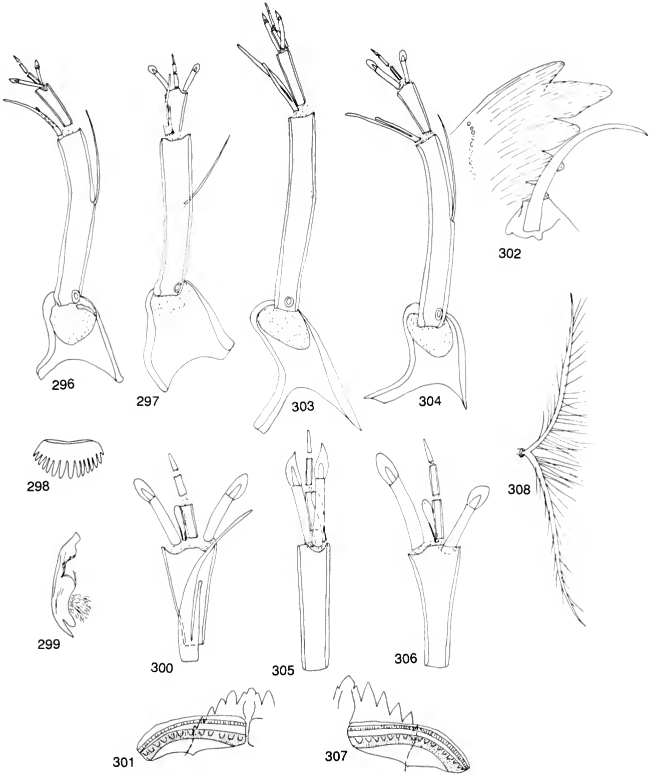
103m L; SA about 175m L; TA ovoid 29μ L x 25μ greatest W; PP with 15 simple claws arranged in "horseshoe" configuration.

SPECIMENS EXAMINED. NP38: 3La, alt. 2520 m.

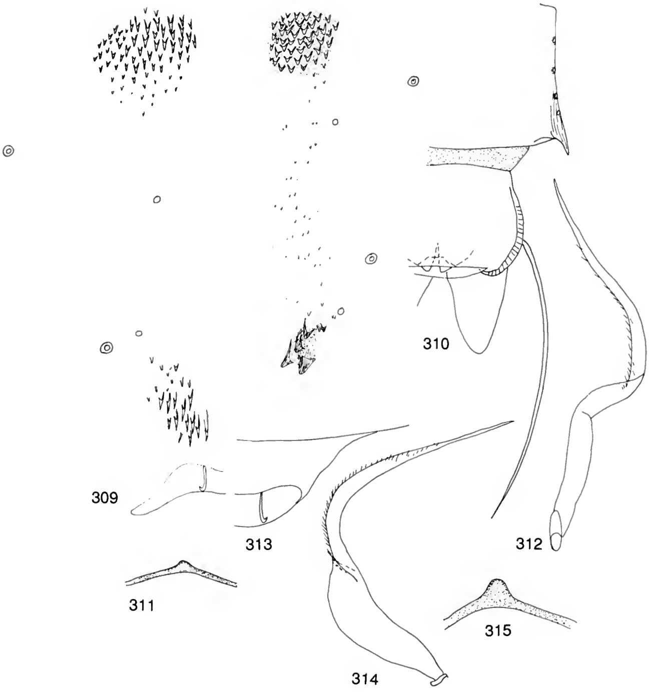
Genus nr. Stempellina

This unusual larva (unfortunately represented by only one poor specimen) is placed near *Stempellina* on the basis of the palmate apicomesal tubercle of the APe (Fig. 289). The strongly sclerotized, sinuate A_1 (Fig. 288), the very large LO (Fig. 290) and tubercle as well as the more sclerotized and anterodorsally scalloped T.I (Fig. 286) are unusual. The Pc (Fig. 287) bear some resemblance to those of *S. montivaga* Geotg. as illustrated in Pinder & Reiss, 1983. Reiss (1984) placed *S. montivaga* Pinder& Reiss 1983 (nec. Geotg.) in a new genus *Neostempellina* and renamed it *N. thienemanni* n. sp.

Larva. Head strongly sclerotized and slightly rugose S3 apparently elongate simple, on globose tubercle (Fig. 293); PE three scale-like apically rounded lobes (Fig. 294); Pm with 3-4 teeth strongly inclined to main axis (Fig. 291); brush present; APe with very large palmate apicomesal tubercle (Fig. 289); tubercle 48μ wide with 30-31 lobes; A_1 (Fig. 288) strongly sinuate and sclerotized; about 44μ long; lateral seta in basal third above CS,A_1; A_2 17+μ with paired LO at apex (Fig. 290); PLO 10μ; LO about 35-35μ L; Bl 80μ L; ABl 134μ; Bl_2 14μ; A_{3-5} not measurable; MD 95μ with apical tooth two laterals and paler dorsal (Fig. 295); SSd very robust; outer margin from base of dorsal tooth, to S_1, raised with some clear areas along margin; PMa of 4-15 lamellae; S_2 four-branched, plumose; A_1/MD 0.46; VmP (Fig. 292) 66μ, appear mesally connected by ridge; M 77μ wide (Fig. 292); VmP/M 0.86; T.I (Fig. 286) appears more sclerotized with sclerotized scallops in anterdorsal corner; only simple setae on T.I; T.II with some plumose setae (see Fig. 272) especially ventrally; Pc sclerotized and dark (Fig. 287); with 2 fine LaPc and some apical setae (most missing); shorter setae present appear multibranched about 124μ L, longer simple setae 190μ L; outer corners of A.IX with short spines (Figs 287); SA about 124μ L with swollen base, TA short rounded (Fig. 287); PP with 15 small simple claws in arc. Case typical for



FIGS. 296-308. 296-302, *Rheotanytarsus* sp. 1, larva. 296, antenna and APe; 297, same, more dorsal view; 298, PE; 299, Pm; 300, detail of apex of antenna, A_2, Bl ABl, SP_2, LO and A_{3-5}, dorsal; 301, VmP and M; 302, apex of MD. 303-308, *Rheotanytarsus* sp. 2, larva: 303, antenna, view as in Fig. 296; 304, same, view as in Fig. 297; 305, detail of A_{2-4} and LO; 306, same more dorsal view; 307, VmP and M; 308, plumose abdominal seta.



FIGS. 309-315. 309-312, *Rheotanytarsus* sp. 2, pupa: 309, spinule pattern A.II; 310, A.VIII, AL and male GS; 311, apical nipple of WP; 312, thoracic horn. 313-315, *Rheotanytarsus* sp. 3, pupa: 313, spinule pattern A.II; 314, thoracic horn; 315, apical nipple of WP.

group; of small stones, slightly curved.

SPECIMEN EXAMINED. NP 38: 1La, alt. 2520 m.

Genus **Rheotanytarsus**

On the basis of pupal characters (Figs. 309-315) the *Rheotanytarsus* species found in Nepal are related to *R. distinctissimus* Brundin. Both pupae found have posterior shagreen spines on A.II (Figs. 309, 313) as shown by Langton 1984 (Fig. 92d) and a granulate FA. The larvae are typical *Rheotanytarsus* with LO (Fig. 300) on short stalks and overall less than length of A_{3-5} (Table 2). The two species, as larvae, differ mainly in size—see Table 2. The partial pupa described as *R.* sp. 3 from NP32 probably belongs to *R.* sp. 1 (also found as larva at NP 32) but no direct association could be made from the specimens available. Most of the specimens of *R.* sp. 1 were associated with the stalked case type with 3 ribs which extend past the case. The exceptions were the two larvae from NP34. These were in soft cases of fine plant flakes and were found on the back of large *Corydalus* larvae. All the specimens of *R.* sp. 2, associated with cases were in soft tube cases of fine plant flakes.

Rheotanytarsus sp. 1

Larva. Head pale brown; PE a single plate (Fig. 298); Pm bifid (Fig. 299) with distinct brush; APe and antenna in Figs. 296-297; lateral seta A_1 44-51μ L; A_2 conical in top view (Fig. 300), straight in lateral view (Fig. 296); 18-22 L; A_3 7-9μ; A_4 4-6μ; A_5 3-4μ; LO 4-6μ L; PLO 12-13μ L; Bl and ABl as in Fig. 300; Bl_2 (Fig. 300) about 11μ L; apex of MD as in Fig. 302; VmP and M in Fig. 301; body with simple hairs and plumose hairs, as in Fig. 308 on abdomen; Pc membranous about 26 x 16μ; apex slightly sclerotized with seven apical setae and two unequal LaPc; TA ovoid 95μ L x 44μ greatest width; PP with 15 simple pale brown claws; other measurements and ratios given in Table 2.

SPECIMENS EXAMINED. NP4: 1La, alt. 1046 m; NP32: 1PrP, alt. 2390 m; NP33: 1La, alt. 2390, NP 34: 2La (ex. *Corydalus*), alt. 2390 m; NP 38: 4La, alt. 2520 m; NP78: 1La, alt. 3500 m.

Rheotanytarsus sp. 2

Pupa. FA rugose; apical seta 333μ; thoracic horn (Fig. 312) 530μ; apical 0.63 with fine short spines; three Pcs (precorneal) setae present; WP brown margined with short, 9μ, nipple (Fig. 311); spine patches of A.II as in Figs. 309; apical recurved hook row of A.II 0.28 segment width; anterior spine patches on A.II-V; A.II,III with three fine lateral setae; A.IV with two fine setae and a caudal filament-like seta; A.V, with three lateral filaments; A.VI, VII with four lateral filaments; A.VIII with three lateral filaments and one fine seta; vortex patches on A.IV-VI; caudolateral spines on A.VIII (Fig. 310); AL (Fig. 310) 130m L with about16 lateral filaments; no dorsal seta discernable; male GS 1.77 AL-L (Fig. 310).

Larva. Head, PE, PrM as in R. sp1; APe and antenna as in Figs. 303, 304; A_2 lateral and dorsal Figs. 305, 306; A_3 9μ; A_4 6μ; A_5 4μ; LO 6-7μ L; PLO 12-1μ; Bl and ABl as in Figs. 303, 304; BL2 11μ (Fig. 303); apex of MD similar to Fig. 302; VmP and M in Fig. 307; body setae, Pc, TA and PP claws as in *R.* sp. 1; other measurements and ratios given in Table 2.

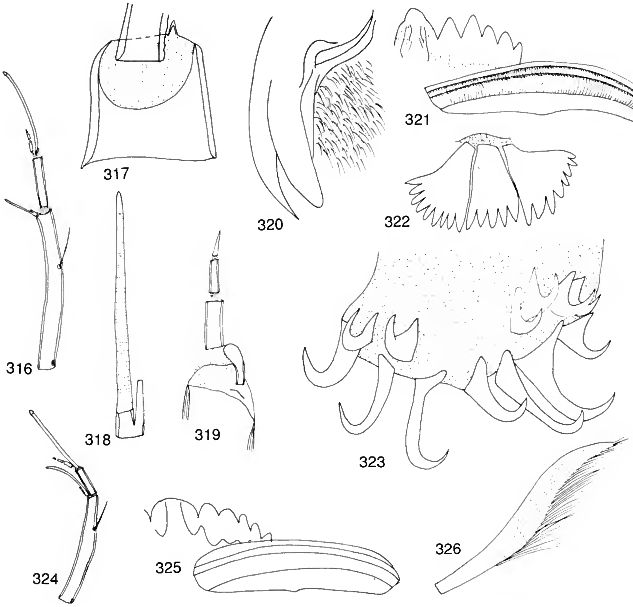
SPECIMENS EXAMINED. Sta. 9: 1La, alt. 1360 m; Sta. 24: 3La, alt. 2135 m; Sta. 25: 1La, alt. 2180 m; Sta. 28: 1La, alt. 2250 m; Sta. 32: 4La; 1PrP; 1 male LaP, alt. 2390 m; Sta. 38: 7La, 1La (III), alt. 2520 m; Sta. 150: 3La, alt. 2470 m.

Rheotanytarsus sp. 3

Pupa. FA rugose apical seta 80μ; RO (Fig. 314) 500μ L, apical 0.59 with fine short spines; three Pcs setae 80-256μ; WP brown margined with distinct nipple (Fig. 315) 20μ L; spine patches A.II as in Fig. 313; apical recurved hook row A.II 0.22 segment width; anterior spine

TABLE 3. Some characters and x of measurements (μ) of the larvae of Nepal *Micropsectra* species. The altitude (m) is rounded to the nearest meter. BR-medium brown: CBR-caudally brown: DBR- dark brown. E-fine; subequal; P-pale; PBR-pale brown; U-unequal; - no data. Numbers in [] after species number gives n for mean unless other wise indicated.

	Micropsectra species												
	2 [6]	3 [1]	4 [2]	4A [3]	5 [3]	5A [2]	6 [3]	7 [2]	8 [4]	8A [1]	9 [1]	10 [1]	11 [6]
APE-L	64.2	51	78	80.3	57	53.5	90.3	82.5	73.0 [3]	88	87	73	73.2 [5]
SAPe-L	6.8	6	12	13.7	17	16.5	18	25.5	20.5	23	25	29	53.8
A_1-L	191.3	143	239	254.7	156	178	231.7	286	22.3	254	219	218	189.3
A_2-L	60.7	39	65.5	83	44	56.5	62.7	91.5	72.7 [3]	88	73	73	60.3
A_{35}-L	25.2	25	30	31.3	24.7	25.5	32.7	30	26.7 [3]	29	29	26	24.6 [5]
Total LO-L	112	86	118.5	117.3	88	110	97.7	148.5	167.5 [2]	76	-	-	54
A_1/A_2	3.163	3.67	3.665	3.08	3.553	3.15	3.7	3.07	3.153 [3]	2.89	3	2.99	3.16
LO/A_{35}	4.480 [2]	3.44	3.96	3.703	3.62	4.315	2.996	4.985	6.220 [2]	5.72	4.93	6.46	4.702 [5]
MD-L	136.6 [5]	110	152.5	134.6	143.7	125.5	207.5 [5]	181	148.3	161	201	150	127.3
A_1/MD	138.4 [5]	1.3	1.57	1.546	1.087	1.415	1.165	1.55	1.543 [3]	1.58	1.09	1.45	1.498
VmP-W	109.8 [5]	92	120.5	123.3	111	92	162	153	118	133	146	124	98.3
M-W	104.4 [5]	88	111	112	109	88	131.3	144.5	104	120	131	111	93.3
VmP/M	1.054 [5]	1.05	1.085	1.1	1.02	1.05	1.233	1.06	1.138	1.11	1.11	1.12	1.058
He-Co	P	P	BR	BR	P	P	DBR	P	P	P	CBR	P	P
A_2-Co	P	P	BR	BR	P	P	DBR	P	P	P	PBR	P	P
PLO-Co	P	P	P	P	P	P	0.44BR	P	P	P	P	P	P
LaPc	U	U	U	U	U	U	E	U	U	U	U	U	U
NO.CL-PP	15	15	65	65	65	15	100	65	35	15	15	35	15
Altitude	2746 [12]	2135	2900 [4]	3465	2480 [1]	2390 [1]	3053	2520 [1]	2385 [2]	2250	3500	2520	1791 [7]



FIGS. 316-326. 316-323, *Micropsectra* sp. 2. larva: 316, antenna; 317, APe; 318, detail of Bl and ABl; 319, detail of Bl_2 and A_{3-5}; 320, apex of Pm; 321, VmP and M; 322, PE; 323, claws of PP. 324-326, *Micropsectra* sp. 3: 324, antenna, larva; 325, VmP and M; 326, RO ex. PrP.

patches an A.II-IV; lateral setae and filaments A.II-VI as in *R*. sp. 2; A.VII, VIII and AL missing.

SPECIMEN EXAMINED. NP32: 1 PEx, alt. 2390 m.

Genus Micropsectra

The genus *Micropsectra* (Reiss 1971) is the dominant genus of Tanytarsini in Nepal, especially above 2000 m. Species of *Micropsectra* are found below 2000 m but there the genus *Tanytarsus* appears to dominate. Reiss also considers that the central asian montane Tanytarsini fauna is very unique. Our data here confirm the first conclusion but, on the basis of the larvae and few pupae found, cannot speak to the second statement. The distinctions between *Tanytarsus* and *Micropsectra* (as given by Pinder & Reiss 1983), as well as the definitions of groups and/or genera within the current generic concepts are at best nebulous. On the basis of the bifid Pm all the following species fall in *Micropsectra* but there is considerable variation in the number and arrangement of the claws of the PP. All the species placed in *Micropsectra* have the following characters in common: (1) antennal pedestal with apical spur; (2) LO/A3-5 at least 3; (3) both LO on apex of A2; LO little wider or longer than pedicel width; (4) Base of A_1 with crenulation, CS,A_1 basal; (5) Pm distally bifid, with brush; (6) MD with apical tooth, 3 inner teeth and a dorsal tooth, all brown. (7) VmP/ M 1.02-1.23; (8) PP with simple claws arranged in simple row of 15 claws to multiple-rows of up to 100 claws; (9) Pc with 7-8 apical setae and two LaPc, generally unequal.

The few pupae found, some associated with the larvae (sp. 1, 2, 4, 5, 10), all have transverse spine patches on A.IV, V grading into variable longitudinal spine patches.

Table 3 summarizes the essential measurements, ratios and characters for all the larvae here placed in *Micropsectra*.

The cases are generally soft, of small plant fragments, though a few such as *M*. sp. 3 are mostly small stones.

Micropsectra sp. 1

This species is known only from the pupal stage. The larval stage could not be indisputably associated, though it is probable that *Micropsectra* sp. 8 or 8A belong with this pupa. The genitalia (Figs. 381, 382) as discerned from a mature male pupa indicate that this species is close to *M. desecta* Reiss.

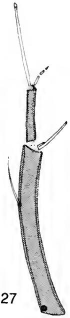
Pupa. FA with slightly conical CT (Fig. 384); seta 93µ; WP brown margined with distinct nipple; RO (Fig. 385) about 315µ L with lateral spines 130µ L; recurved spine row on A.II 0.38 segment width; A.II with extensive shagreen of fine spinules with caudomesal clear area; shagreen of A.III-V as in Fig. 397; A.VI with faint shagreen pattern as on A.V; caudolateral comb A.VIII pale (Fig. 383); A.II, III with three lateral setae as in Fig. 395; A.IV with one dorsal seta and two ventral short filaments as in Fig. 396; A.V with three, A.V I, VII with four and A.VIII with five LS; AL 185µ L with 35µ lateral filaments and one dorsal; dorsal distant from lateral filaments.

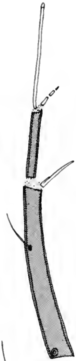
SPECIMENS EXAMINED. NP26: 4 male, 7 female P, alt. 2250 m.

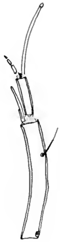
Micropsectra sp. 2

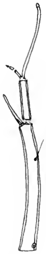
This was the most widespread of all the Nepalese *Micropsectra* species. The larva and pupa were clearly associated. The larva is character-

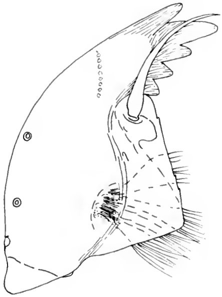
FIGS. 327-339. 327-328, *Micropsectra* sp. 4, larva: 327, antenna; 328, APe; 329 claws of PPl. 330-332 *Micropsectra* sp. 4A, larva: 330, antenna; 331, APe; 332, MD. 333-336, *Micropsectra* sp. 5, larva: 333, antenna; 334, APe; 335, Pc; 336, VmP and M. 337-339, *Micropsectra* sp. 5A, larva: 337, antenna; 338, APe; 339, claws of PP.

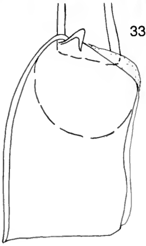

327

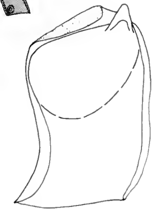

330

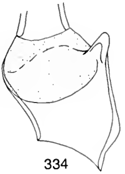

333

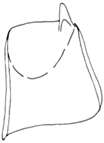

337

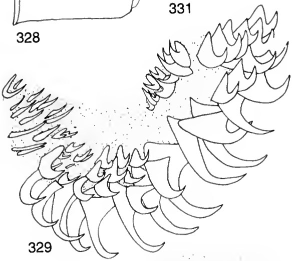

332

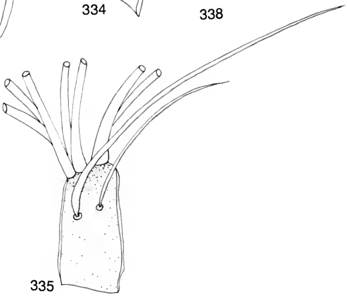

328

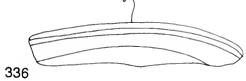

331

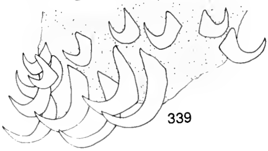

334


338


329


335


336


339

ized by the very short spur of the APe. It is separated from *Micropsectra* sp. 3 by the longer antennal measurements (see Table 3) and the pupal abdominal shagreen (Fig. 398).

Pupa. CT of FA low dome-like as in Fig. 384; WP faintly brown margined; nipple barely indicated; RO (Fig. 387) 463µL with lateral spines 81-93µ L; A.II with extensive shagreen; shagreen of A.III-V as in Fig. 398; A.VI with very faint shagreen; lateral setae and filaments of A.II-VIII as in *Micropsectra* sp. 1; caudolateral comb A.VIII (Fig. 386) pale brown; AL 168-185µ L; about 25 lateral filaments and one dorsal, placed as in *Micropsectra* sp. 1; male GS 1.68 AL-L; female 1.20.

Larva. APe 54-70µ L; spur (Fig. 317) 6-9µ L; Pm apex as in Fig. 320; PE as in Fig. 322; A_1 (Fig. 316) 169-204µ.; lateral seta A_1 0.62-0.72 from base; A_2 58-66µ; total LO-L 110-114µ; LO/A_{3-5} 4.40-4.56; Bl 54-66µ (Fig. 318); ABL 13 ; A_1/A_2 2.90- 3.52; Bl_2 (Fig. 319) 8µ; A_1/MD 1.23-1.46; VmP (Fig. 321) 108-114µW; VmP/M 1.05-1.09; Pc as in Fig. 335; 7-8 apical setae and two unequal LaPc; claws of PP in "horseshoe" configuration (Fig. 323); other characters and measurements given in Table 3.

SPECIMENS EXAMINED. NP14: 3La (III, alt. 1548 m; NP 18:1La, (III), alt. 2000 m; NP25: 2La, alt. 2180 m;NP26: 11La, 2 PrP, 4 male P, 1 female PEx, alt. 2250 m; NP37- 1La, alt. 2480 m; NP39 - 3La, alt. 2520 m; NP 41: 1La; 1La (?III), alt. 2520 m; NP 47: 1La, alt. 2660m; NP 51: 3 La, alt. 2675 m; NP 89: 1La (?III), alt. 3995 m NP90: 3La, alt. 4025 m; NP98: 2 La, 3La (III), alt. 4100 m; NP150: 1La, 12La (III), alt. 2470 m.

Micropsectra sp. 3

This species is represented by a single PrP in which the pupal abdominal shagreen pattern was discernible (Fig. 399). The larva is very close to Micropsectra Sp. 2, differing in the smaller antenna (Fig. 324) and smaller VmP (Fig. 325). The RO of the pupa (foreshortened in the PrP) is shown in Fig. 326. The essential larval measurements, ratios and characters are given in Table 3.

SPECIMEN EXAMINED. NP24: 1 PrP, alt. 2135 m.

Micropsectra sp. 4

This and the following species (M. sp. 4A) are distinguished by the medium brown head and the brown A_1 and A_2. They are in all probability variants of the same species but due to the longer A_2 of *M.* sp. 4A it was felt desirable to keep them separate for the present.

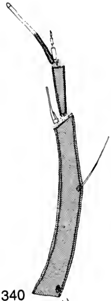
Larva. APe 77-79µ L; spur (Fig. 328) 12µ L; A_1 (Fig. 327) 237- 241µ; lateral setae A_1 0.62-0.69 from base; A_2 61-70µ; A_{3-5} 29- 31µ; total LO 114-123 ; A_1/A_2 3.44-3.89; LO/A_{3-5} 3.68-4.24; MD 152-153µ; A_1/MD 1.56-1.58; VmP 118-124µ; M 111µ; VmP/M 1.05- 01.12; Pc similar to Fig. 335, with 7-8 pale apical setae; PP claws as in Fig. 329; mean of measurements and ratios, and other characters given in Table 3.

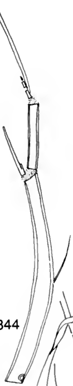
SPECIMENS EXAMINED. NP40: 1La, alt. 2520 m; NP43: 1La, alt. 2525 m; NP71: 1La, alt. 3400 m; NP73: 1La, alt. 3455 m.

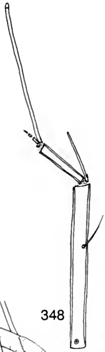
Micropsectra sp. 4A

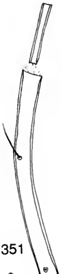
Larva. Color of head an antenna as *M*. sp. 4; APe (Fig. 331) 76-83µ L; spur 13-15µ L; A_1 (Fig. 330) 241-289µ; lateral seta A_1 0.59-0.66µ from base; A_2 73-88µ; A_{3-5} 31-32µ; total LO 111-121µ; A_1/A_2 2.66-3.30; LO/A_{3-5} 3.58-3.78; MD (Fig. 332) 161-169µ; A_1/MD 1.38-1.76;

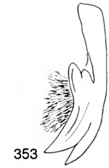
FIGS. 340-354. 340-343, *Micropsectra* sp 6, larva: 340, antenna; 341, APe; 342, VmP and M; 343, PE. 344-347, *Micropsectra* sp. 7 larva: 344, antenna; 345, APe; 346, VmP and M; 347, claws of PP. 348-350, *Micropsectra* sp. 8, larva: 348, antenna; 349. APe; 350, VmP and M. 351-354, *Micropsectra* sp. 8A, larva: 351, antenna; 352, detail of base of A_1; 353, Pm; 354, apex of APe.

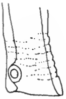

340

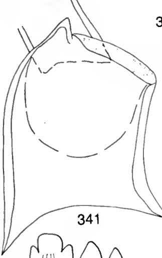

344

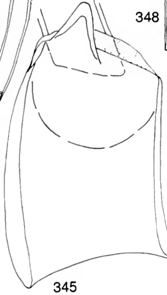

348

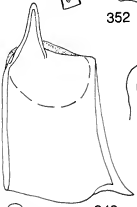

351

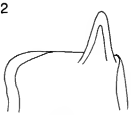

353

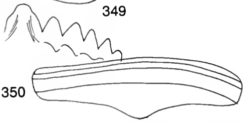

352

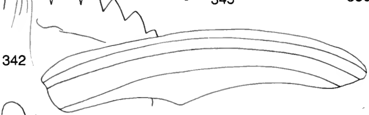

341

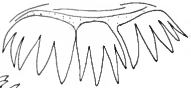

345

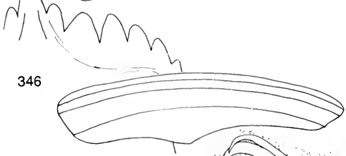

349

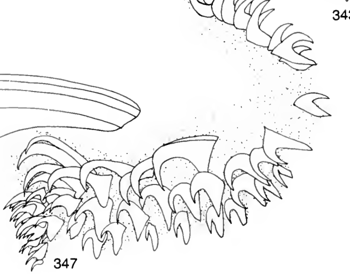

354

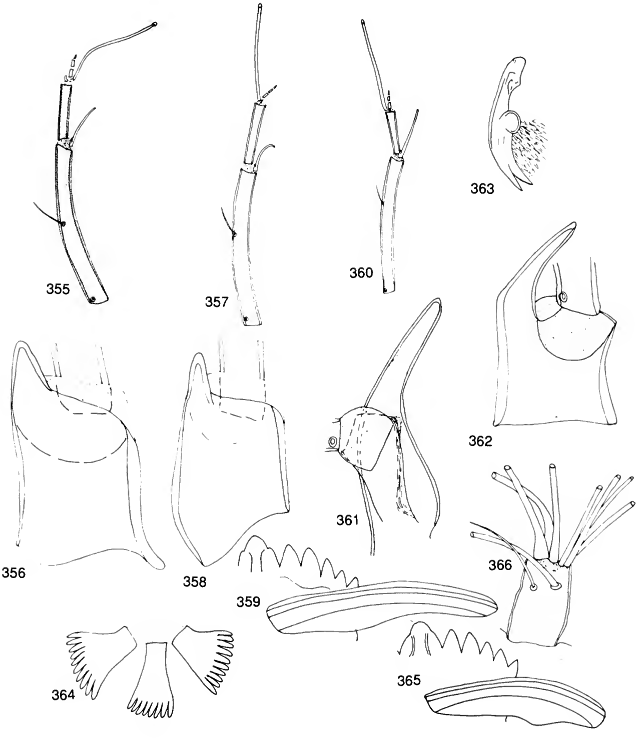

350


342

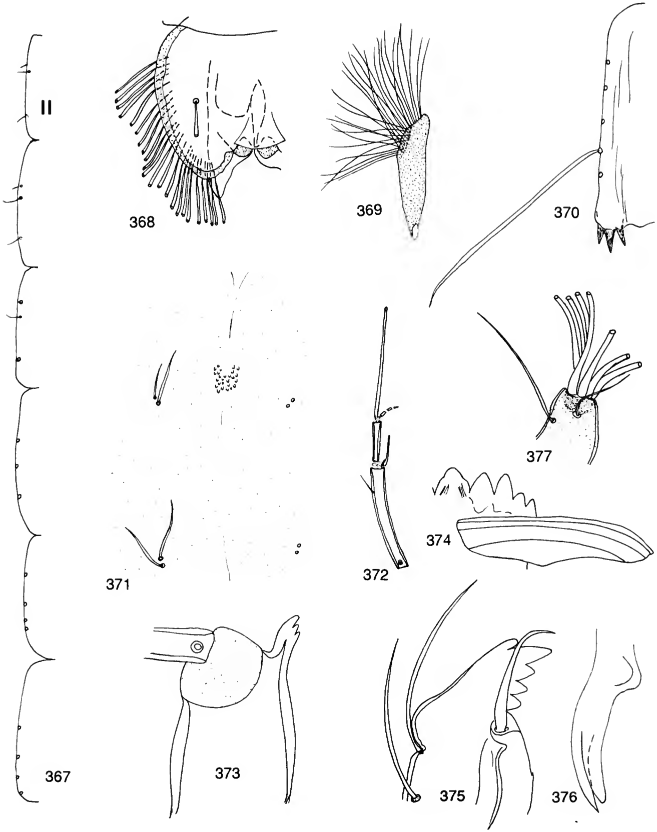

343


346

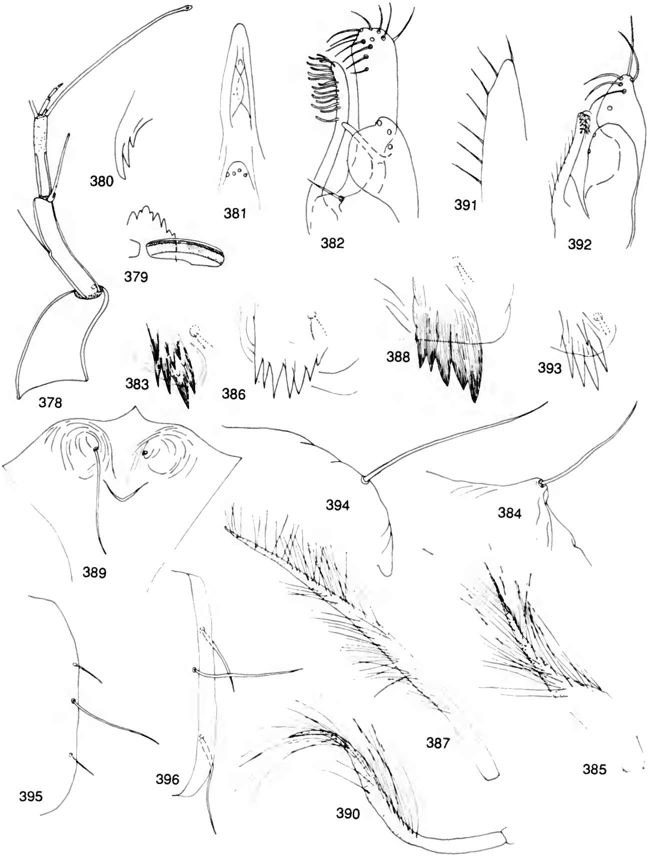

347



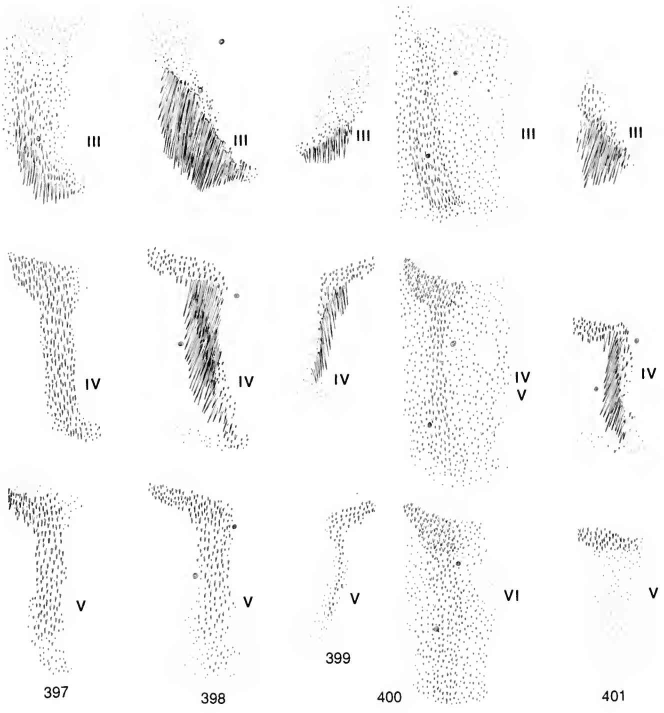
FIGS. 355-366. 355-356, *Micropsectra* sp. 9, larva: 355, antenna; 356, APe. 357-359, *Micropsectra* sp. 10, larva. 357, antenna; 358. APe; 359. VmP and M. 360-366, *Micropsectra* sp.11, larva: 360, antenna; 361, APe, lateral; 362, APe, dorsal; 363, Pm; 364, PE; 365, VmP and M; 366, Pc.



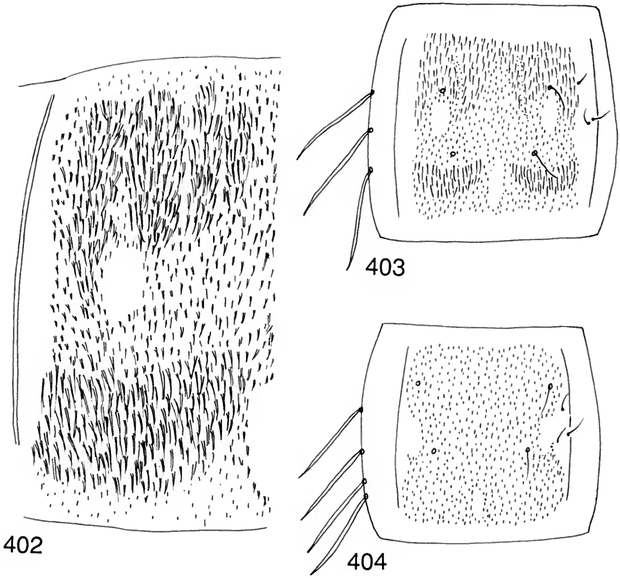
FIGS. 367-377. Genus nr. *Micropsectra*, 367-371, pupa: 367, lateral setae and filaments AII-VII; 368, AL; 369, RO; 370. A.VIII with caudolateral comb; 371, Dcs setae and notal tubercles. 372-377, larva: 372, antenna; 373, APe; 374, VmP and M; 375, MD; 376, PE; 377, Pc.



FIGS. 378-396. 378-380, *Tanytarsus* sp., larva: 378, APe and antenna; 379, VmP and M; 380. Pm. 381-385, *Micropsectra* sp.1, pupa: 381, 382, male genitalia ex. pupa; 383. caudolateral comb A.VIII; 384. CT; 385, RO. 386-387, *Micropsectra* sp. 2, pupa: 386, caudolateral comb A.VIII; 387, RO. 388-390 *Miropsectra* sp. 5, pupa: 388 caudolateral comb A.VIII; 389, FA with CT; 390, RO. 391-396, *Micropsectra* sp. 10, pupa: 391. apex of Gs, ex pupa; 392, appendages 1, 2, 2a male genitalia ex. pupa; 393, caudolateral comb. A.VII; 394 CT; 395, lateral setae A.III; 396, lateral setae, A.IV.



FIGS. 397-401. *Micropsectra* pupal spinule patterns: 397, A.III- V, *M*. sp. 1; 398, A.III-V, *M*. sp. 2; 399, A-III-V, *M*. sp. 3; 400, A.III-VI, *M*. sp. 5; 401, A.III-V, *M*. sp. 10.



FIGS. 402-404. Genus nr. *Micropsectra*, pupa: 402, detailed spinule pattern A.III; 403, spinule pattern A.V; 404, spinule pattern A.VI.

VmP 119-131μ W; M 108-117μ W; VmP/M 1.07-1.12; Pc similar to Fig. 335; PP claws like Fig. 329; mean of measurements and ratios, and some additional characters given in Table 3.

SPECIMENS EXAMINED. NP 71: 1La, alt. 3400 m; NP76: 1La, alt. 3495 m; NP134: 2La (?III), 21 PrP, alt. 3500 m.

Micropsectra sp. 5

This species and *M.* sp. 5A are very similar in APe spur length (Figs. 334, 338) and the short APe. They differ in the number of claws of the PP (Table 3) and the longer A_2 and LO of *M.* sp. 5A. A PEx has been associated with *M.* sp. 5.

Pupa. FA as in Fig. 389; CT appear as low domes; RO (Fig. 390) 333μ L with lateral spines 130 μ L; WP with dark brown margin and short nipple; lateral setae and filaments of A.,II-VIII as in *M.* sp.1; shagreen pattern of A.III-VI as in Fig. 400; A.VI pattern like V but very faint; caudolateral comb A.VIII black-brown (Fig. 388) with 5-6 spines; AL brown, 204u; marginal LS-AL 45-48; last two LS at apex of AL more like setae; dorsal LS close to marginal LS; male GS brown with pale tip; >1.55x AL-L.

Larva. APe 55-58μ (Fig. 344); spur 15-18μ; A_1 (Fig. 333) 153- 162μ; lateral setae A_1 0.67-

0.74 from base; A_2 41-47 μ; A_{3-5} 22- 29 μ; total LO 88μ A_1/A_2 3.45-3.73; LO/A_{3-5} 3.03-4.00; Bl 55 μ MD 139-146 μ; A_1/MD 1.05-1.11; VmP (Fig. 336) 109-114 μ W; M 105-114 μ W; VmP/M 1.00-1.04 (Fig. 335); Pc (Fig. 335) with seven pale apical setae; claws of PP similar to Fig. 339; other characters and mean of measurements and ratios given in Table 3.

SPECIMENS EXAMINED. NP37: 2La, 2La (III), 1PrP, 1 male PEx, alt. 2480 m.

Micropsectra sp. 6

This is perhaps the most unique of the *Micropsectra* species found in Nepal. It has a wholly dark brown head, dark, brown A_1, A_2 and the base of the PLO (Fig. 340) is sclerotized and pigmented. The VmP (Fig. 342) is unusually wide.

Larva. APe(Fig. 341)80-95μ; spur 18 μ L; PE (Fig. 343) robust with long teeth; A_1(Fig. 340) 213-241m; lateral setae A_1 0.62-0.71 μ from base; A_2 56-55 μ; A_{3-5} 31-35 μ; total LO 95-99 μ; basal 0.44 of LO sclerotized and pigmented (Fig. 340); Bl 47 μ; ABl 15 μ; A_1/A_2 3.65-3.80; LO/A_{3-5} 2.83-3.19; MD 203-212μ; A_1/MD 1.14-1.19; VmP 150-168 μ W; M 123-140 μ W; VmP/M 1.20-1.28; Pc membranous with 7-8 apical setae; lateral setae of Pc fine and subequal; PP with large "horseshoe" of simple claws; other characters and mean of measurements and ratios given in Table 3.

SPECIMENS EXAMINED. NP55: 1La, 2La (?III), alt. 2830 m; NP56: 1La, alt. 2830m NP 127: 2La, 2La (?III), alt. 3500 m.

Micropsectra sp. 7

This taxon is separated on the basis of the very long antenna (Fig. 344), the stout robust spur of the APe (Fig. 345) and the very wide VmP (Fig. 346).

Larva. APe 80-85 μ (Fig. 345); spur robust, 25-26 μ L; A_1 (Fig. 344) 270-292 μ lateral seta A_1 0.51-0.52 μ from base; A_2 88-95μ; A_{3-5} 29-31 μ; total LO 146-153μ; A_1/A_2 3.07; LO/A_{3-5} 4.94-5.03; MD 175-187 μ; Bl 70 μ; A_1/MD 1.54-1.56; VmP 153 μ W; M 143-146 μ W (Fig. 346); VmP/M 105-1.07; Pc typical for genus; claws of PP (Fig. 347); other character measurements and ratios given in Table 3.

SPECIMENS EXAMINED. NP 42: 2La, alt. 2520 m.

Micropsectra sp. 8

This and the following species (*M.* sp. 8A) are probably, like *M.* sp. 4 and 4A, variants of the same species. They differ only in the longer antenna (Fig. 351) of *M.* sp. 8A and the apparent lower no. of claws on the PP of that species. Except for one specimen from Sta. NP40, both were found only at NP26 and possibly represent the larva of *M.* sp. 1, known only from the pupal stage.

Larva. APe 73 μ (Fig. 349); spur 19-22 ; A_1 194-234μ; lateral seta A_1 0.60-0.68 from base; A_2 72-73m; A_{3-5}26-28 μ; total LO 164-171 μ ; A_1/A_2 3.04-3.21μ.; LO/A_{3-5} 5.86-6.58; MD 146-153μ; A_1/MD1.50-1.60; Bl 61-66 μ; VmP 111-123 μ W (Fig. 350); M 95-111 μ. W; VmP/M 1.11-1.17; Pc typical for genus; PP with 35m claws; other characters and mean of measurements and ratios given in Table 3.

SPECIMENS EXAMINED. NP26: 6La, alt. 2250 m NP40: 1La (III), alt. 2520 m.

Micropsectra sp. 8A

Larva. APe as in Fig. 354; $A_1$and A_2 in Fig. 351; base of A_1 as in Fig. 352; PrM shown in Fig. 353; Bl 76 μ; measurements and ratios of single specimen in Table 3.

SPECIMENS EXAMINED. NP2: 1PrP, alt. 2250m.

Micropsectra sp. 9

This taxon, represented by a single mature specimen is distinguished by its pale brown A_1, A_2 (Fig. 355) and the dark caudal head margin. It resembles *M.* sp. 4 but has a much longer spur on the APe

Larva. APe and spur as in Fig. 356; antenna in

Fig. 355; characters and ratios given in Table 3.

SPECIMENS EXAMINED. NP77: 1La (?II), 1PrP, alt. 3500 m.

Micropsectra sp. 10

This species with its long spur on the antennal pedestal (Fig. 358) was associated with a male pupa from the same station by means of a well developed abdominal shagreen. This pattern (Fig. 401) is quite distinct from the other pupae found in Nepal (Figs. 397-400). The female gentalia, as far as it could be distinguished in the mature male pupa (Figs. 391-392) lack appendage la and appear to be close to *M. digitata* Reiss.

Pupa. CT (Fig. 394) appears low, dome-like; WP with brown margin and a small nipple; RO (distorted in single specimen) appears similar to Fig. 390; about 370 µ L with lateral spines 130µ. recurved hook row on A.II 0.35 segment width; shagreen of A.,III-V as in Fig. 401; AII, III with three lateral setae, one dorsal, two ventral (Fig. 395); A.IV laterally with dorsal setae and two filament-like ventrals (Fig. 396); AV with three, A.VI, VII with four and A.VIII with five LS; caudolateral comb A.VIII, Fig. 394; AL 133 µ L; male GS 2.03 AL-L; one filament on disc of AL, distant from lateral filaments; AL with 22-24 laterals.

Larva. APe and spur as in Fig. 358; antenna in Fig. 357; VmP and M shown in Fig. 359; other characters, measurements and ratios given in Table 3.

SPECIMENS EXAMINED. NP38; 3La, La(III), 1 male P, alt. 2520 m.

Micropsectra sp. 11

This species has the longest spur on the APe of any species here assigned to this genus. It was widespread (seven stations) and was found at lower altitudes (1462-2390 m) than the other *Micropsectra* species collected. This might suggest that this taxon should be placed in *Tanytarsus*. Pinder and Reiss (1983) cite *T. brundini* Lindeberg as having a long tapering spur. The Pm (Fig. 363) of this species has only two narrow apical teeth and it is on this basis that it is assigned to *Micropsectra*.

Larva. APe 73-74 µ L; spur (Figs. 361, 362) 44-58 µ; A_1 (Fig. 360) 178-209 µ; lateral seta A_1 0.63-0.65 from base; A_2 55-73m; A_{3-5} 23-29 µ; total LO 107-124µ ; total LO/A_{3-5} 4.28-5.39; MD 124-131 µ; A_1/MD 1.40-1.61; Bl 54 µ; ABl 12 µ; VmP (Fig. 365) 95-101 µ W; M 91-99µ W; VmP/M 1.00-1.13; Pc (Fig. 366) with seven apical setae and two unequal laterals; claws of PP similar to Fig. 339; other characters and mean of measurements and ratios in Table 3.

SPECIMENS EXAMINED. NP 8: 3La, alt. 1530 m; NP12: 7La, alt. 1462 m; NP14: 2La, alt. 1548 m; NP16: 1La, alt. 1610 m; NP18: 1La, alt. 2000 m; NP22: 1PrP, alt. 2000 m; NP35: 1La, alt. 2390 m.

Genus nr. **Micropsectra**

The genus represented by this taxon is clearly close to *Micropsectra* on the basis of the APe and antenna (Fig. 372) and the bifid Pm (Fig. 376). It differs in the lobed spur of the APe (Fig. 373) and the distinct lateral hump on the MD (Fig. 375). In this latter character it resembles *Parapsectra* (Reiss, 1969). The pupa has a very distinctive overall shagreen pattern (Fig. 402) and a RO resembling that of *Cladotanytarsus* (Fig. 369). The group of small tubercles between the Dcs1,2 pairs (Fig. 371) is distinctive. The lateral setae and filaments of the abdomen (Fig. 367) as well as the AL structure (Fig. 368) are as in *Micropsectra*.

Pupa. RO as in Fig. 369; 148 µ L x 37 µ wide; lateral setae about 150 µ L; WP brown margined with small nipple Dcs1-4 and notal group of tubercles as in Fig. 371; Dcs1 56µ; Dcs2 70µ; Dcs3 74 ; Dcs4 (SaS) 67 µ; Pcs (2) fine 111 µ; Laps 67 µ; poss. Maps 130µ; A.II with general shagreen ; A.III-V with pattern as in Figs. 402-403; pattern A.VI Fig. 404; lateral abdominal setae and LS filaments as in Fig. 367; A.II, III with one dorsal and two ventral fine setae; A.IV with a dorsal seta and two ventral filaments (as in Fig. 367) 159 µ L; A.V with 3LS, A.VI, VII with four LS and A.VIII (Fig. 370) with five LS; LS on

A.VIII 259 μ; caudolateral comb. A.VIII, with only three spines (Fig. 370); AL 185 μL with 27-30 LS (148 μ L) and one dorsal LS (Fig. 368); female GS 1.12 AL.

Larva. APe 55 μ L (Fig. 373); apical spur trilobed, (Fig. 373) 22-24 μ L; A_1 (Fig. 372) 129-131μ;A_1/A_2 2.57-2.62; LO/A_{3-5} 4.29-5.24; S3 simple; PE bilobed (Fig. 376); MD (Fig. 375) with distinct hump above S_1, 120μ ; A_1/MD 1.03; VmP (Fig. 374) 88-95 μ W; M 88-89μ W; VmP/M 1.00-1.07; Pc (Fig. 377) membranous with seven apical setae and two fine laterals; PP with 60+ simple claws in "horseshoe" configuration.

SPECIMENS EXAMINED. NP26: 1 female PEx, 2 PrP, alt. 2250 m.

Tanytarsus

Only one larva found could be placed in *Tanytarsus* as defined by Pinder and Reiss (1983). It had the three-branched Pm (Fig. 380) and A_2 apically membranous (Fig. 378).

Larva. Head pale brown; PE not discernable; PM with three apical teeth (Fig. 380) and brush; APe 45 μ L without apical spur (Fig. 380); A_1 58 μ L with lateral seta 0.50 from base; Bl about 23μ; ABl 9 μ; A_2 38 μ L; apical 0.46 membranous (Fig. 380); A_3 9 μ; A_4 7m; A_5 4 μ; A_{3-5} 22 μ; LO and stalk 95 μ; LO/A_{3-5} 4.32; MD 63μ with an apical tooth, two lateral teeth and a paler dorsal tooth; A_1/MD 0.92; VmP (Fig. 379) 44m wide; M 38 μ wide; VmP/M 1.16; Pc membranous, 25 μ Lx 15 μ W; with 7-8 apical pale setae and two fine LaPc; Ta conical 61 μ L x 18 μ greatest W; a constriction 0.20 from base; PP with about15 pale simple claws.

SPECIMEN EXAMINED. NP38: 1La, alt. 2520 m.

General Discussion

The chironomid fauna of the Kali Ghandaki, the Marsyandi and their tributaries, as can be seen in Table 4, is a rich one. It is quite comparable to that reported by Thienemann (1941) from Lapland, the Alps and Middle European Mountains. This is especially noteworthy when one considers that the Nepal collections were a one-shot collection by collectors who were not chironomid specialists. Thienemann's material represents a much greater collection effort by specialists.

The Podonominae appear to be absent from the area of Nepal collected. The status of the presumed Himalayan podonomine genus *Neopodonomus* is discussed above. The only confirmed podonomines described from the Himalaya area are from Northern Burma (Brundin 1966).

The Tanypodinae fauna, dominated by the Thienemannimyia group and *Trissopelopia*, were generically diverse but represented by few specimens. As Table 4 demonstrates, there were three times as many genera in Nepal as in the Bolivian Peruvian Altiplano. The 10 species found in Nepal representing 10% of the overall chironomid fauna are comparable to the 14 species, representing 9% of Chironomidae fauna reported by Thienemann (1941). The altiplano tanypodine fauna, of only three species, was relatively depauperate. *Macropelopia*, common in Europe, was not found in Nepal, but*Apsectrotanypus* which Thienemann (1941) reported from middle European Mountains as *Ps. trifascipennis* Zett. was present in Nepal. The *Thienemannimyia* group is common in both faunas.

The genera comprising the Nepalese tanypodine fauna are all found in the Northern Nearctic and Palaearctic Regions. Had the Nepalese Tanypodinae specimens been submitted with erroneous locality data from the northern U.S. and southern Canada there would have been no reason to doubt their veracity. At the generic level there is no evidence of endemism in the Nepal Tanypodinae.

The diamesine fauna of Nepal, as represented by the present material, includes four of the nine Holarctic genera for which immatures have been associated. The genera that are not represented in this material are all known to occur widely in the Palaearctic and, at least, locally in the Nearctic. It is reasonable, therefore, to expect them to occur in the ecologically diverse Himalayan region. Collections from additional biotopes (particularly oligotrophic lakes in the case of *Protanypus*) and from different times of the year would be likely to include most of the other genera. Only three genera of Diamesinae (*Diamesa, Pseudodiamesa* and *Sympotthastia*) are recorded from the Oriental Region (Sublette and Sublette, 1973), mostly from adjacent areas of montane India.

The diamesine faunas of Nepal, the Bolivian-Peruvian Altiplano and Lappland are compared in Table 4. The Nepal collections and those reported by Thienemann (1941) for Lappland show a very similar percent composition: 9% of chironomid species in Nepal and 10% of chironomid species in Lappland. The Altiplano fauna (Roback and Coffman 1983) demonstrates a much reduced (2% of chironomid species) role for Diamesinae.

The Orthocladiinae fauna of Nepal, as represented by this material, is composed mainly of Holarctic elements. All 24 of the named genera represented in the collections are widely distributed in both the Palaearctic and the Nearctic Regions, and many of them are also known from extra-Holarctic regions. It is possible that the unusual species considered here as belonging to *Pseudosmittia* may better be placed in another, closely related, genus. If so, it would be the only orthoclad genus among those collected that could possibly be endemic to Nepal. At the species level, the most likely endemic taxa are: Brillia sp., *Eukiefferiella* sp., *Nanocladius* (*Plecopteracoluthus*) sp., *Paracricotopus* sp., *Parametriocnemus* sp. 4, *Pseudosmittia* sp., both species of *R.* (*Psilocricotopus*) and Poss. *Thienemanniella* sp. The occurrence of *Paraphaenocladius* cf. *pseudirritus* and Orthocladiinae sp. (*Paraphaenocladius* sp. C ? of Strenzke (1950) apparently represent interesting disjunctions with the western Palaearctic. However, both of these species are probably widely distributed through the little known mountainous areas connecting the western Palaearctic with the Himalayan area. The most striking disjunction revealed is that of *N.* (*Plecopteracoluthus*). The three previously known species in this subgenus are extra- Palaearctic, with two species known from the Nearctic and one from the Neotropical Region. The absence of this taxon from the relatively well-known western Palaearctic may indicate a distribution pattern in the relatively poorly-known eastern Palaearctic.

Although the 24 named genera that are contained within this material represent approximately one-third of the Holarctic genera of Orthocladiinae for which immature stages are known (about 39% of Holarctic genera when exclusively marine and Nearctic genera are not included), the orthoclad fauna must still be considered to be genus poor. Intensive collection efforts in other geographical areas of the Holarctic almost always yield many more genera. However, the absence of many widespread Holarctic genera in these collections most probably reflects only their absence in the collections, not their absence in Nepal. Sublette and Sublette (1973) list 17 non-marine orthoclad genera as occurring in the Oriental Region. Three of these genera are known from Nepal and were not found in the collections considered here: *Acricotopus*, *Heterotrissocladius* and the apparent Himalayan endemic *Asclerina* Reiss (1968). Of 15 named orthoclad genera recorded by Coffman (unpublished) from the hill ranges of southern India there are 3 wide-spread genera that are not represented in the Nepalese collections: *Cardiocladius*, *Parakiefferiella*, and what appears to be *Paratrissocladius*.

At the species level, the 50 species that were collected represent 52% of the chironomid fauna. This value is reasonably close to the values for Orthocladiinae from the Bolivian-Peruvian Altiplano and Lappland (Table 4).

TABLE 4. Summary of chironomidae fauna found in Nepal (NP) compared with that found in the altiplano (BP) and modified data from the northern and more montane European streams (LAPP).

	Number of Genera		Number of Species		
	BP [1]	NP	BP [1]	NP	LAPP [2]
Podonominae	2	0	4(7)	0(0)	3(2)
Tanypodinae	3	9	3(5)	10(10)	14(9)
Diamesinae	1	4	1(2)	9(9)	15(10)
Orthocladiinae	19	25	33(58)	50(52)	96(62)
Chironominae	6	11	16(28)	28(29)	26(17)
Chironomini	2	3	12(21)	5(5)	10(7)
Tanytarsini	4	8	4(7)	23(24)	16(10)
Totals	31	49	57	97	154

[1] From Roback and Coffman, 1983.
[2] From Thienemann, 1941.

The Chironominae fauna of Nepal is comparable in species number to that reported from northern Europe by Thienemann (1941), but represents a higher percentage of the fauna (29% vs. 17%). This may be a result of the lower Diamesinae and Orthocladiinae fauna in Nepal. Compared to the altiplano fauna, the percentage is about the same but 12 more species were found in Nepal.

Within the Chironominae fauna in both Nepal and Europe the Tanytarsini are represented by more species than the Chironomini. The species and generic diversity within the Tanytarsini are, however, greater than that reported by Thienemann (1941) (23 vs. 16 species and 8 vs. 6 genera). Of the valid genera cited by Thienemann (1941), only *Lithotanytarsus* and *Phaenopelma* were not found in Nepal. *Lundstroemia* is a synonym of *Micropsectra* (see Ashe 1983). Most of the genera listed here other than *Micropsectra*, *Tanytarsus* and *Rheotanytarsus* have been recorded from Europe and/or North America (Pinder and Reiss 1983). When the Nepal fauna is compared with that of the altiplano the picture is completely reversed. Here (BP) the Tanytarsini fauna was very sparse (only four species and four genera) and the Chironomimi fauna was represented by 12 species and 2 genera. Of the Tanytarsini genera found in the altiplano, only *Paratanytarsus* was not found in Nepal. The taxon labelled *Tanytarsus* n. sgn. from the altiplano appears close to *Micropsectra* sp. 11. As noted under the species description the latter is probably a *Tanytarsus*.

The Chironomini fauna in Nepal was rather sparse. This is not surprising as few ponds or slow water habitats were collected. The genera *Microtendipes*, *Polypedilum* sg. *Polypedilum*, and *Chironomus* were all recorded by Thienemann (1941).

The altiplano Chironomini fauna consisted of only two genera: five species of *Chironomus* and seven *Polypedilum*, all subgenus *Tripodura*. The validity of the subgenera of *Polypedilum* is in question, but the larval type figured in Roback and Coffman (1983) and generally assigned to *Tripodura* has not been recorded from the Palaearctic region.

Overall the Nepalese chironomid fauna is essentially a typical Holarctic assemblage with very few, if any endemic genera. Most of the species although undescribed, can easily be placed in European and North American genera and even some described species are found both in Nepal and Europe. The general pattern of the number of genera and species within each subfamily and tribe is comparable to that found in similar habitats in Europe and North America.

ACKNOWLEDGEMENTS

We should like to acknowledge our debt to the collectors of the Nepalese Chironomidae, Drs. Goulden and Horwitz of the Academy of Natural Sciences of Philadelphia and Dr. Jacquez of the State University of New York at Stony Brook. Dr. Bill Stark of Mississippi College, at Clinton, Mississippi identified the stonefly hosts of N. (*Plecopteracoluthus*) sp. The National Science Foundation (Grant BSR 83-0839) supported the field work, in Nepal, of Drs. Goulden and Horwitz.

LITERATURE CITED

Ashe, P. 1983. A catalogue of chironomid genera and subgenera of the world including synonyms. Entomologica Scandinavica Supplement No. 17: 1-68.

Bode, R. W. 1983. Larvae of North American *Eukiefferiella* and *Tvetenia* (Diptera: Chironomidae). Bulletin of the New York State Museum. 452: 1-40.

Brundin, L. Über die Metamorphose der Sectio Tanytarsariae Connectentes (Dipt: Chironomidae)Arkiv för Zoologi 41A: 1-22, 7 pl.

Brundin, L. 1966. Transantarctic relationships and their significance as evidenced by chironomid midges. Kungl. Svenska Vetenskapsakademiens Handlingar, Fjarde Serien. Band 11(1): 472 pp.

Caldwell, B. A. 1985. *Paracricotopus millrockensis* a new species of Orthocladiinae (Diptera: Chironomidae) from the Southeastern United States. Brimleyana 11:161-168.

Chaudhuri, P.K. 1981. A new genus of podonomine midge (Chironomidae) from Bhutan. Systematic entomology 6:373-376.

Chaudhuri, P.K. 1982. Orthocladid midges of the genus *Orthocladius* van der Wulp (Diptera, Chironomidae) from Eastern Himalayas. Annales Zoologici, Polska Academia Nauk 36: 491-500.

Chaudhuri, P.K. and M. Ghosh. 1980. The Orthocladiinae (Diptera: Chironomidae) of India. Genus *Cricotopus* van der Wulp. Aquatic Insects 2(3): 147-152.

Chaudhuri, P. K., D. K. Guha, and S. K. Das Gupta. 1981. Taxonomic studies of Chironominae (Diptera: Chironomidae) Genus *Polypedilum* Kieffer. Tijdschrift voor entomologie 124: 111-147.

Chaudhuri, P. K., D. C. Sinharay and S. K. Das Gupta. 1979. A study on Orthocladiinae (Diptera: Chironomidae) of India. Part II. Genus *Limnophyes* Fabr. Aquatic Insects 1(2): 106-137.

Coffman, W. P. 1983. Thoracic chaetotaxy of chironomid pupae (Diptera: Chironomidae). In Proceedings of the 8th International Symposium on Chironomidae. Memoirs of the American Entomological Society 34:61-70.

Cranston, P. S. 1982a. A key to the larvae of the British Orthocladiinae (Chironomidae). Freshwater Biological Association Scientific Publ. 45: 152 pp.

Cranston, P. S. 1982b. The metamorphosis of *Symposiocladius lignicola* (Kieffer) n. gen., n. comb., a wood-mining Chironomidae (Diptera). Entomologica Scandinavica 13: 419-429.

Cranston, P. S. 1984. The taxonomy and ecology of *Orthocladius* (*Eudactylocladius*) *fuscimanus* (Kieffer), a hygropetric chironomid (Diptera). Journal of Natural History 18: 873-985.

Cranston, P. S., D. R. Oliver and O. A. Saether. 1983. The larvae of Orthocladiinae (Diptera: Chironomidae) of the Holarctic region—keys and diagnoses. Entomologica Scandinavica supplement 19: 149-291.

Edwards, F. W. 1924. Some British species of *Corynoneura* Entomologists Monthly Magazine 9: 181-189.

Edwards, F. W. 1928. Some nematocerous Diptera from Yunnan and Tibet. The Annals and Magazine of Natural History Ser. 10: 671-703.

Edwards, F. W 1929. British non-biting midges. Transactions of the Royal Entomological Society, London 77: 279-430.

Epler, J. H. 1986. A novel new Neotropical *Nanocladius* (Diptera: Chironomidae), symphoretic of*Traverella* (Ephemeroptera: Leptophlebiidae). The Florida Entomologist 69(2): 319-327.

Fittkau, E. J. 1962. Die Tanypodinae (Diptera: Chironomidae) (die tribus Anatopyniini, Macropelopiini und Pentaneurini. Abhandlungen zur Larval-systematik der Insekten NR. 6, xi + 453 pp.

Goetghebuer, M. 1935. Ceratopogonidae et Chironomidae récoltés pour la première fois en Belgique. Bulletin et Annales de la Societé Entomologique de Belgique 75: 413-418.

Guha, D. K. and P. K. Chaudhuri. 1982. Record of *Polypedilum* Kieffer (Diptera: Chironomidae) in Bhutan and India with a new species from India. Journal of the Bombay Natural Society 79: 635-638.

Halvorsen, G. .A. and O.A. Saether. 1987. Redefinition and revision of the genus *Tokunagaia* Saether 1973 (Diptera: Chironomidae). Entomologica Scandinavica Supplement No. 29 : 173-188.

Hirvenoja, M. 1973. Revision der Gattung *Cricotopus* van der Wulp und ihrer Verwandten (Diptera: Chironomidae). Annales Zoologici Fennici 10: 1-363.

Kieffer, J. J. 1909. Diagnoses de nouveaux chironomides d'Allemagne. Bulletin de la Societé d'Histoire Naturelle de Metz 26: 37-56.

Kieffer, J. J. 1910. Étude sur les Chironomides des Indes Orientales. Memoirs of the Indian Museum 11: 181-242.

Kieffer, J. J. 1911a. Descriptions de nouveaux Chironomides de l'Indian Museum de Calcutta. Records of the Indian Museum 6: 113- 177.

Kieffer, J. J. 1911b. Les Chironomides (Tendipédidae) de l'Himalaya et d'Assam. Records of the Indian Museum 6:319-349.

Kieffer, J. J. 1911c. Nouveaux Tendipédides du groupe *Orthocladius* (Dipt.) 1st Note. Bulletin de la Societé Entomologique de France: 181-187

Kieffer, J. J. 1911d. Nouveaux Tendipédides du groupe *Orthocladius* (Dipt.,) 2nd note. Bulletin de la Societé Entomologique de France: 199-202.

Kieffer, J. J. 1912. Quelques nouveaux Tendipédides (Dipt.) obtenus d'éclosion, 2nd note. Bulletin de la Societe Entomologique de France: 101-103.

Kownacki, A. and R. Zosidze. 1973. *Parametriocnemus stylatus adzharicus* n. ssp. (Chironomidae, Diptera). Bulletin de l'Academie Polonaise des Sciences, Serie des Sciences biologiques Cl II. vol. 21: 127-130.

Lanoton, P. H. 1984. A key to pupal exuviae of British Chironomidae. MARCH, Cambridgeshire: 1-324.

Lehmann, J. 1969. Die europäischen Arten der Gattung Rheocricotopus Thien, und Harn. und drei neue Artvertreter dieser Gattung aus der Orientalis (Diptera: Chironomidae). Archiv fur Hydrobiolgie 66: 348-381.

Lundbeck, W. 1898. Diptera groenlandica. Videnskabelige Meddelelser fra den Naturhistoriske forening i Kjobenhavn fra Aaret : 236-314.

Molnar, P. 1986. The geologic history and structure of the Himalaya. American Scientist 74(2): 144-154.

Oliver, D. R. 1983. The larvae of Diamesinae (Diptera: Chironomidae) of the Holarctic region - keys and diagnoses. Entomologica Scandinavica Supplement 19: 115-138.

Oliver, D. R. 1986. The pupae of Diamesinae (Diptera: Chironomidae) of the Holarctic region - keys and diagnoses. Entomologica Scandinavica. Supplement 28: 119-137.

Oliver, D. R., D. McClymont, and M. E. Roussel. 1978. A key to some larvae from the Mackenzie and Porcupine River Watersheds. Canadian Fisheries and Marine Service Technical Report No. 791:iv + 73 pp.

Oliver, D. R. and M. E. Roussel. 1982. The larvae of *Pagastia* Oliver (Diptera: Chironomidae) with descriptions of three Nearctic species. Canadian Entomologist 114: 849-854.

Oliver, D. R. and M. E. Roussel. 1983. Redescription of *Brillia* Kieffer (Diptera: Chironomidae) with descriptions of Nearctic species. Canadian Entomologist 115: 257-279.

Pinder, L. C. V. and F. Reiss. 1983. The larvae of the Chironominae of the Holarctic Region. Entomologica Scandinavica Supplement No. 19: 293-435.

Potthast, A. 1915. Über die Metamorphose der *Orthocladius*- Gruppe. Archiv fur Hydrobiologie. Suppl. Bd. 2: 243-376.

Reiss, F. 1968. Neue chironomiden-Arten (Diptera) aus Nepal. Khumbu Himal 3:55-73.

Reiss, F. 1969. Die neue, europaisch verbreitete Chironomidengattung *Parapsectra* mit einem brachypteren Artvertreter aus Mooren (Diptera). Archiv fur Hydrobiologie 66: 191-211.

Reiss, F. 1971. Tanytarsini-Arten (Chironomidae, Diptera) aus Nepal mit der Neubeschreibung von funf *Micropsectra* und drei *Tanyarsus*-Arten. Khumbu Himal 4: 131-151.

Reiss, F. 1984. *Neostempellina thienemanni* n. gen., n. sp., eine europaische Chironomid mit gehaustragenden Larven. Spixiana 7: 203-210.

Roback, S. S. 1978. The immature chironomids of the Eastern United States III. Tanypodinae-Anatopyniini Macropelopiini and Natarsiini. Proceedings of The Academy of Natural Sciences of Philadelphia 132: 176-217.

Roback, S. S. 1980. The immature chironomids of the Eastern United States IV. Tanypodinae-Procladiini. Proceedings of The Academy of Natural Sciences of Philadelphia 132:1-63.

Roback, S. S. 1986. The immature chironomids of the Eastern United States VIII. Pentaneurini-Genus *Nilotanypus*, with the description of new species from Kansas. Proceedings of the Academy of Natural Sciences of Philadelphia 138(2):443-465.

Roback, S. S. and W. P. Coffman. 1983. Results of the Catherwood Bolivian-Peruvian Altiplano Expedition part II. Aquatic Diptera including montane Diamesinae and Orthocladinae (Chironomidae) from Venezuela. Proceedings of The Academy of Natural Sciences of Philadelphia 135: 9-79.

Saether, O. A. 1969. Some Nearctic Podonominae, Diamesinae, and Orthocladiinae (Diptera: Chironomidae). Bulletin of the Fisheries Research Board of Canada 170:1-154.

Saether, O. A. 1977a. Taxonomic studies on Chironomidae: *Nanocladius*, *Pseudochironomus*, and the *Harnischia* complex. Bulletin of the Fisheries Research Board of Canada 196:1-143.

Saether, O. A. 1977b. The female genitalia in Chironomidae and other Nematocera: morphology, phylogenies, keys. Bulletin of the Fisheries Research Board of Canada 197:VIII + 209 pp.

Saether, O. A. 1980a. The females and immatures of *Paracricotopus* Thienemann and Harnisch, 1932, with the description of a new species (Diptera: Chironomidae). Aquatic Insects 2: 129-145.

Saether, O. A. 1980b. Glossary of chironomid morphology terminology. Entomologica Scandinavica Supplement No. 14: 1-51.

Saether, O. A. 1985. A review of the genus *Rheocricotopus* Thienemann and Harnisch, 1932 with the description of three new species (Diptera: Chironomidae). Spixiana Supplement 11: 59- 108.

Saether, O.A. and G. A. Halvorsen. 1981. Diagnoses of *Tvetenia* Kieff., *Dratnalia* n. gen. and *Eukiefferiella* Thien. emend., with a phylogeny of the *Cardiocladius* group. Entomologica Scandiavica, Supplement No. 15: 269-285.

Saether, O.A. and E. Willassen. 1987. Four new species of *Diamesa* Meigen 1935, from the glaciers of Nepal. Entomologica Scandinavica Supplement No. 29 : 189-203.

Sawedal, L. and E. Willassen. 1980. Redescription of *Micropsectra borealis* (Kieffer, 1922) n. comb (Diptera: Chironomidae) Entomologica Scandinavica 11: 56-60.

Serra-Tosio, B. 1971. Contribution á l'étude taxonomique, phylogénétique, biogéo-graphique et écologique des Diamesini (Diptera, Chironomidae) d'Europe. Thése Presenteé a L'Université Scientifique et médicale de Grenoble T. I:1-303, T.II: 304-462.

Soponis, A. R. 1977. A revision of the Nearctic species of*Orthocladius* (*Orthocladius*) van der Wulp (Diptera: Chironomidae). Memoirs of the Entomological Society of Canada 102:1-187.

Steffan, A. W. 1965. *Plecopteracoluthus downesi* gen. et sp. nov. (Diptera: Chironomidae), a species whose larvae live phoretically on larvae of Plecoptera. Canadian Entomologist 97:1323-1344.

Strenzke, K. 1950. Systematik, Morphologie und Ökologie der terrestrischen Chironomiden. Archiv für Hydobiologie Suppl. Bd. 18:207-414.

Sublette, J. and M. Sublette. 1973. Family Chironomidae. Pages 389-422 *in* M. Delfinado and D. Hardy (Eds.) A catalog of the Diptera of the Oriental Region. Vol. 1. University Press of Hawaii, Honolulu.

Tapponier, P. 1986. A tale of two continents. Natural History 95(11): 56-65.

Thienemann, A. 1936. Chironomidenlarven und-puppen der Yale North India Expedition. Zoogeographica 3: 145-158.

Thienemann, A. 1941. Lapplandische Chironomiden und ihre Wohngewasser. Archiv fur Hydrobiologie Suppl. Bd. 17: 1-253.

Tokunaga, M. 1959. A new midge from Kashmir (Diptera: Tendipedidae). Akitu 8: 21-23.

Thienemann, A. 1966. Some nematocerous Diptera of the north-east of Afghanistan. Results of the Kyoto University Scientific Expedition to the Karakoram and Hindukush, 1955, Vol. 8:273-286.

Zavřel, J. 1938. Chironomidarum larvae et nymphae I. Spisy vydávané prirodovédeckov Fakultou Masarykovy University Brne 268:1-10.

Zetterstedt, J. W. 1840. Insecta Lapponica, Sectio Tertia, Diptera. Lipsiae Sumtibus Leopoldi Voss: col. 1-1140.

Proceedings of The Academy of Natural Sciences of Philadelphia 139: 159-209, 1987

The Immature Chironomids of the Eastern United States IX. Pentaneurini - Genus *Labrundinia* with the Description of some Neotropical Material

SELWYN S. ROBACK
Department of Entomology
The Academy of Natural Sciences of Philadelphia
19th & the Parkway, Philadelphia, PA 19103

ABSTRACT.— Keys and descriptions are given for the larvae and pupae of the New World species of *Labrundinia*. The larvae and pupae of *L. pilosella*, *L. becki*, *L. maculata*, *L. neopilosella* and vars., *L. johannseni* and *L. virescens* are described from North America. In addition, from North America, *L.* sp. 3 nr. *virescens*, described from the pupa only, is possibly associated with *L.* sp. 4 described from the larva only. The same is also possibly true for *L.* sp. 10 (pupa) and *L.* sp. 6 (larva). Two species are described from Cuba as larvae only (*L.* sp. 2, *L.* sp. 8), two from Trinidad as PEx (*L.* sp. 11, *L.* sp. 12); two from Venezuela as PEx (*L.* sp. 1, *L.* sp. 3) and five from Colombia as larvae (*L.* sp. 1, *L.* sp. 2 nr. *virescens*, *L.* sp. 5, *L.* sp. 7, *L.* sp. 9). Data on the distribution and ecology of *Labrundinia* are given. [distribution, ecology, immature stages, *Labrundinia*, Nearctic, Neotropical, Pentaneurini, systematics, Tanypodinae]

This is the thirteenth in a series on the immature chironomids of the eastern United States. These are Roback (1974, 1976, 1977, 1978, 1980, 1981, 1985, 1986 a,b), Roback and Coffman (1977), Roback and Moss (1978) and Roback and Tennessn (1978). The primary collecting and rearing effort by the author was limited to the eastern United States. Additional *Labrundinia* specimens, as will be noted below, have been generously donated or loaned by other individuals or institutions for inclusion in this study. These specimens cover most of the North America continent, north of Mexico. Inasmuch as the genus *Labrundinia* is known to be abundant in the Neotropical Region and material was available from Cuba, Trinidad, Venezuela and Colombia, it did not seem at all logical to artificially stop the geographic coverage of this work at the Rio Grande. As will be noted in the descriptions, at least two species (*L. virescens* and *L.* sp. 6) appear to be U.S. representatives of primarily Neotropical species groups within *Labrundinia*. Consequently the keys and descriptions cover all the *Labrundinia* known to me from the Neotropical and Nearctic Regions.

Labrundinia specimens are relatively well represented in collections and a great deal of material was available for this study. Unfortunately, as is usually the case, there are never enough fully reared male adults or indisputably associated life stages as one would like in order to clearly understand the varation within any given species and to delineate any possible subspecies.

I am indebted to the following institutions and individuals for the loan and/or donation of specimens used in this study. Specimens in the collections of the Academy of Natural Sciences of Philadelphia are labelled [ANSP].

[BAZ] Department of Environmental Control, Lincoln NE (Mr. Ken Bazata).

[CNC]	Canadian National Collections, Ottawa ONT (Dr. D. R. Oliver).
[COFF]	Dr. W. P. Coffman, Univ. of Pittsburgh, PA.
[DP]	Duke Power Co., Huntersville NC (Mr. T. Wilda, Mr. P. Wingo).
[FDER]	Florida Dept. of Environmental Regulation, Punta Gorda FL (Mr. Robert P. Rutter).
[FLSM]	Florida State Museum, Gainesville FL (Mr. Frank Mead).
[GDNR]	Georgia Dept. of Naural Resources, Atlanta GA (Mr. Broughton Caldwell).
[KA]	University of Kansas, Lawrence KA (Dr. L. Ferrington Jr.).
[NC]	North Carolina Division of Environmental Management, Raleigh NC (Mr. David Lenat).
[USNM]	United States National Museum, Washington DC (Dr. R. V. Peterson)
[WAT]	Clemson University, Clemson, SC (Mr. Charles N. Watson Jr.).
[WINN]	Freshwater Institute of Canada, Winnipeg MAN (Mr. Bodhan Bilyj).

I am additionally indebted to Mr. William Beck Jr, Ms. Darlene Judd, Dr. V. Hruska and Mrs. Marcia Brauning for the donation of material for this study.

Abbreviations and Terminology

The following abbreviations and terminology are used in the descriptions, figures and tables. With some exceptions they follow Saether (1980). The pupal thoracic setae follow Coffman (1983) and the abdominal setae Fittkau (1962). The ventral head setae follow Kowalyk (1985) and the measurements of the Li (O, M_t, I_t) are illustrated in Roback (1985, Fig. 86). The measurements used to delineate the furcate PP claw of *Labrundinia* are illustrated in Fig. 211.

PUPA

AeT	aeropyle tube in ANi
AL	anal lobe
ANi	apical nipple, RO
A.I-IX.	abdominal segments
CS	campaniform sensillum
D_{1-5}	dorsal abdominal setae
Dcs	dorsocentral setae, thorax
FA	frontal apotome
GS	genital sheaths
$L_{1,2}$	lateral abdominal setae
LS_{1-5}	lateral filaments A. VII, VIII and AL
RA	respiratory atrium
RO	respiratory organ
Sas	supraalar seta (Dcs4), thorax
$V_{1,2}$	ventral abdominal setae
WP	wing pads

LARVA

A-C	measurements of PPCL
a-e	apical appendages of palpus
A_{1-4}	antennal segments
ABl	acessory blade, A_1
AP	anterior parapods
ApT	apical tooth of MD
AR	antennal ratio A_1/A_{2-4}
Bl	blade of A_1
Bl_2	blade of A2 (=L0)
Cl	claw
CS	campaniform sensillum
CVS	caudoventral spur group of head
DmT	dorsomental teeth
H	head
IC	head W/L
I_t	inner teeth of Li
Lc	lacinia
LCh	lacinial chaetae
Li	ligula
LV	labial vesicle
LVS	lateroventral spur group of head
MacC	caudal head maculation
MacV	ventral head maculation
MApp	medioventral appendage of prementum
MD	mandible
Mt	median tooth of Li
O	outer teeth of Li (=Li-L)
P1	main palpal segment
P_b	apical palpal segments
Pc	procercus
P_g	palpiger
PH	pecten hypopharyngis
Pl	paraligula
PP	posterior parapod
PPCl	furcate claw of PP

Pr	pseudoradula
S_{1-3}	lateroventral mandibular setae
S9,S10	lateroventral head setae
SA	supraanal setae
SBS	subbasal seta of PP
SS_m	submental setae
St	stipes
TA	anal tubules
VM	ventromentum
VP	ventral pore

SPECIMENS EXAMINED

m	male
f	female
La	larva
P	pupa
PEx	pupal exuviae
PrP	prepupa
A	adult

MEASUREMENTS

D	depth
L	length
W	width

All larvae are fourth instar unless indicated by II, second instar, and III, third instar, in parentheses.

Localities described in Roback (1976) are indicated by boldface number in parentheses after river or creek name.

GENERIC DIAGNOSIS

The adult descriptions of Fittkau (1962) and Roback (1971) are sufficient to delineate the adult stage of *Labrundinia*. The pupal and larval descriptions require some amplification over those given by Fittkau and Murray (1986) and Fittkau and Roback (1983). The apical nipple of the *Labrundinia* respiratory organ with the generally simple aeropyle tube (Figs. 26, 33, 42) and club-shaped apex resembles that of *Ablabesmyia* s. str. (Roback, 1985, Figs. 166-175). The apical nipple of *L.* sp. 10 (Figs. 66, 67) with its convoluted aeropyle tube resembles that of *Guttipelopia* but this is merely a superficial resemblance as the two genera are not otherwise closely related. The same is undoubtedly true as regards *Labrundinia* and *Ablabesmyia* but here the morphology of of the apical nipple is almost identical in both genera. In both genera the plastron plate is very reduced, especially in the subgenus *Ablabesmyia* and most of *Labrundinia*. In *Labrundinia*, except for *L.* sp. 11 (Fig. 70), the presence of a true plastron could be questioned certainly from the functional point of view. The following characters add to or modify those in the above mentioned papers.

Pupa

(1) Respiratory organ may be club-shaped (Figs. 18-25, 30-32) wedge shaped (Figs. 35-41) or semi-bulbous (Figs. 46-54, 55-57, 66); (2) apical nipple present with generally simple aeropyle tube (Figs. 26-28), apex of areopyle tube with club-like expansion (Figs. 42-45) into very small plastron, only sp.11 (Fig. 70) with distinct larger plaston; (3) clear area of RO lacking; (4) reticulation of respiratory organ, if present, very indistinct; (5) external spinules of respiratory organ more basally concentrated (Fig. 29); (6) anal fins narrow, apically attenuate (Figs. 78-94), spines only on outer margin; (7) shagreen sparse and small (Fig. 12); (8) tergite A. VIII projects over base of AL (Figs. 78, 83, 88, 89,91).

Larva

(1) pseudoradula abutting (Figs. 123-126) or inserted into (Figs. 127-131) sclerotized internal ridge; (2) d-seta of labrum annulate (Figs. 119-120); (3) antennal ratio 2.0-3.5; (4) head smooth (Figs. 94-103) or pustulate (Figs. 104-111); in either case LVS (Figs. 95-98) or LVS and CVS (Figs. 107-111) groups may be present. Head narrowed anterior to LVS group; (5) ligula with I_t shorter than either M_t or O (Figs. 177-205); (6) one claw of posterior prolegs unevenly forked; lower spur more elongate than upper (Figs. 211-217); (7) SBS generally with lateral spinules (Figs. 218-221, 225-227) or larger flag-like.spinule groups near base (Figs. 234-241).

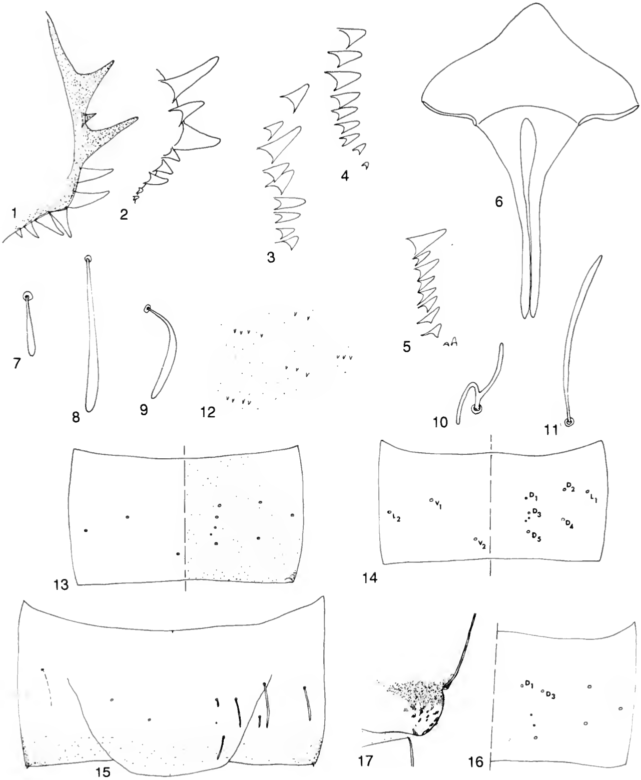
Morphology

Pupa. The frontal apotome is relatively uniform within *Labrundinia* and shaped as in Fig. 6. The thorax is pale brown with the MAps, LAps, Pcs and Dcs setae tubular and apically narrowed as in Figs. 10, 11. Dcs 1 (Fig. 10) is unusual in being furcate about 0.25 from its base. All the setae are soft and membranous and usually collapse or are distorted in mounting.

The respiratory organs are club-shaped (Figs. 18, 30), wedge- shaped (Figs 37, 39) hatchet-shaped (Fig. 73) to ovoid (Figs. 55, 56). There is a faint reticulate pattern present but it is difficult to discern except in perfect mounts. Some surface spines are present, mostly in the basal third (Fig. 29). The respiratory atrium in the club-shaped RO generally fills the RO except for a shallow to deep (Figs. 61, 65) apical notch. The aeropyle tube originates from the upper margin of the notch and is variable in length—shorter in *L. becki*, *L. pilosella* and *L. maculata* (Figs. 26, 33, 43) and longer in *L. neopilosella* (Figs. 51-53), *L. virescens*, *L.* sp. 12 and *L.* sp. 3 nr. *virescens.* The aeropyle tube extends into the short apical nipple (Figs. 28, 45) and expands into a generally small plastron (about 4 µ diameter). It is very similar to the situation in *Ablabesmyia* (Roback 1985). In *L. virescens* and *L.* sp. 3 nr. *virescens* there is a caudo-mesal groove in the RA giving the RA an S-shape (Figs. 59, 62). *L.* sp. 11 from Trinidad may illustrate an intermediate stage (Figs. 68, 69) in the development of this RO. In the ovoid respiratory organs of *L. johannseni* and *L.* sp. 10 (Figs. 55, 56) the notch, if present, cannot be seen due to the difficulty in getting a lateral AeT view in mounting. The larger apical nipple and convoluted aeropyle tube of *L.* sp. 10 (Fig. 67) are unusual. All species have a triangular lobe at the base of the RO (Figs. 32, 40, 68). A distinct thoracic comb of 8-10 spines is present (Figs. 1-5). In *L. virescens, L.* sp. 3 nr. *virescens* and *L.* sp. 10 the comb is more arcuate with the second spine clearly smaller than the unusually large first and third (Figs. 1, 2).

The wing pads are clear to pale-brown pigmented. In *L.* sp. 10 and *L.* sp. 12 the veins are more distinctly pigmented. The scar of A.I (Fig. 71) is present but not strongly pigmented. The abdomen is unpigmented but may be pigmented as in Figs. 13, 15, 77. This variation from clear to Fig. 13 can exist within a single species. In *L.* sp. 10 there is a caudal brown band across the segment (Fig. 15). The abdomen is generally flat but in *L. virescens*, *L.* sp. 3 nr. *virescens* and *L.* sp. 10 (Fig. 15) at least A. III-VII have a distinct hump-most pronounced in *L.* sp. 10 (Fig. 15). In all species A. VIII is produced caudally over the base of the GS and AL (Figs. 82, 88,89). The abdominal shagreen consists of small spines (2 µ L), generally single but occasionally paired (Fig. 12). This shagreen is present dorsally and ventrally on A. VII, VIII and as lateral bands on sternites II-VI. Tergites II-VI are generally bare. The anal lobes lack shagreen except at their very base. Slightly hyaline, somewhat pigmented tubercles appear to be present at the caudolateral corners of A.II-V (Fig. 17). The abdominal setae are tubular, apically narrowed and rounded (Figs. 7-9). They are arranged, on A.IV as in Figs. 13-16. D_3 may be caudad (Figs. 13, 14) or more laterad of D_1 (Figs. 15, 16). A.II, VII with four D setae, A.III-VI with five D setae. L_1 appears to be present or A.I or II-VI and L_2 on A.I-VII. V_1 and V_2 appear to be present on A.II-VII. A.VII bears four LS filaments and A.VIII, five. Their placement is given in Tables 6-8.

The anal lobes are each about 2.5-4.0 as long as their basal width. Laterally they are more sclerotized and darker, mesally more pale and membranous (Figs. 80, 89, 94). The LS filamants of the anal lobes (Figs. 80, 87) bear sticky sheaths. Their placements is given in Tables 6-8. The anal lobes bear spines only on the outer margin caudad of the second LS filament. There are 7-14 spines present and the longest spines may be from 7-31 µ long. *L. virescens* (Fig. 90) bears the longest spines in the genus. The genital sacs of the male are elongate, tapering (Figs. 80, 83, 85, 89). Basally they appear more sclerotized and darker, apically pale and membranous.



FIGS. 1-17. Pupa. 1-5, thoracic comb: 1, *L.* sp. 10; 2, *L.* sp. 3 nr. *virescens*; 3, *L. maculata*; 4, *L. pilosella*; 5, *L. becki*; 6, frontal apotome, *L. becki*; 7-9, *L. pilosella*, setae A.IV; 7, D_1; 8, D_3; 9, D_4. 10-11, *L. pilosella*, thoracic setae: 10, Dcs1; 11, Dcs2; 12, shagreen A.VII, *L.* sp. 10. 13-16, abdominal setae and pattern A.IV: 13, *L. pilosella;* 14, *L. becki*; 15, *L.* sp. 10; 16, *L. maculata;* 17, caudolateral tubercle, A.IV, *L.* sp. 10.

They are slightly shorter (Figs. 80, 83, 85), subequal (Figs. 82,94) or clearly longer than the anal lobes (Figs. 78, 89). The female genital sacs are a quarter to a third the length of the anal lobes (Fig. 93). Many pupal measurements, ratios and their means are given in Tables 6-8.

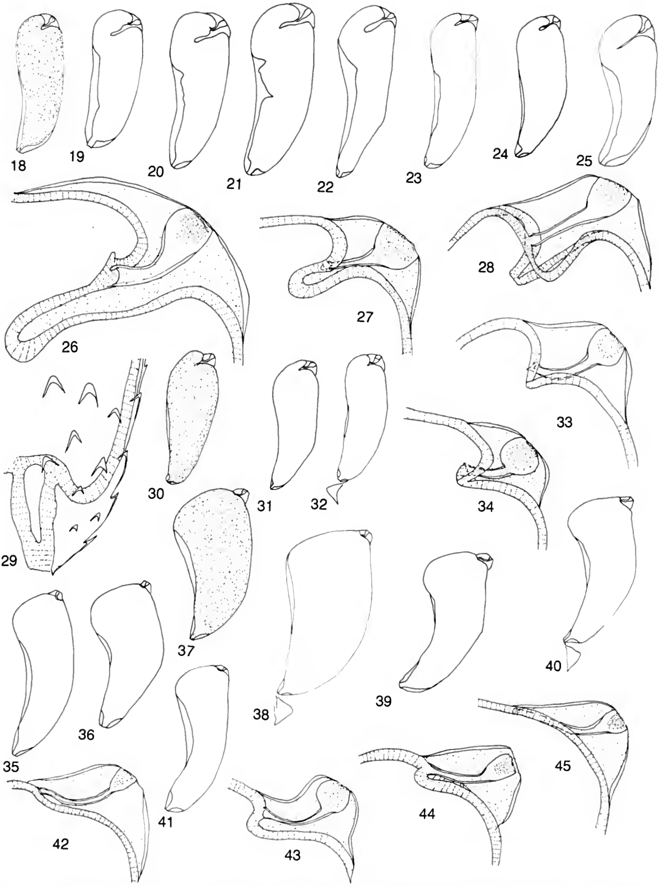
Larva. The larval head is shaped as in Figs. 95-111, generally slightly to sharply narrowed anterior to LVS group of spurs behind eyes. The IC is generally less than 0.55. Most specimens are slightly flattened in mounting giving an artificially high IC (up to 0.68). Some which I have personally mounted are in the 0.50 range. The head may be compeletly covered with short pustules (Figs. 104-111), with or without additional distinct patches of larger spurs. There are two distinct spur patches. These are the LVS group located below and behind the eye spots (Figs. 95-98) and the CVS group located caudoventrally on the head Fig. 110. Except for *L. pilosella* (Fig. 106), all heads seen have at least the LVS group (Figs. 95-105), with or without additional overall pustules. Figs. 95-105, 107-111 show the various combinations of pustules, LVS and CVS groups found. The CVS group has not been found without the LVS group also being present. On those head with pustules and LVS and CVS groups the precise number of spurs is difficult to determine as they blend into the pustules. The numbers given (Table 5) are those which seem to be larger than the surrounding pustules. The head may be immaculate (Figs. 96, 97, 99, 100, 104, 105) with the caudal portion brown (Figs. 95, 98, 106) with a transverse brown band (Fig. 101-103) or with a mesoventral amoeboid brown area Figs. 107-111. The lateroventral head setae (S9, S10,SSm) and ventral pore (VP) are arranged as in Figs. 121,122. The general pattern of the head setae are shown in Figs. 99, 103, most appear to be simple. The terminology follows Kowalyk (1985). The labrum is as in Fig. 119. The a and d seta are on shorter pedestals than in *Ablabesmyia* (Roback 1985, Fig. 11). The d- seta is unique in being distinctly annulate (Figs. 119, 120). The labral chaetae are present along most of the labral margin (Fig. 119).

The antenna is as in Fig. 132. A_1 is generally brown and striate except for the basal 0.35 which is paler (Figs. 132, 133). Its length/mesal width is about 11.0. The CS,A_1 (Fig. 134) is small (about 3.6m in diameter) and often indistinct. It is generally placed 0.80-0.90 length of A_1 from its base. The AR varies from 1.87-3.50. A_2 is narrow, elongate, about 12-14 times as long as its mesal width. It may be darkened (Fig. 136). A_3 and A_4 are short, Bl_2 ovoid, SP_2 small and more sessile (Figs. 135, 136). Bl and ABl are subequal in length to A_{24} (Figs. 135, 136). The basal ring of the Bl is about 2.5-3.0 longer than wide. The Bl and ABl are easily distorted in mounts and difficult to measure accurately.

The mandible (Figs. 161-176) is moderately curved with two inner teeth. The more distal is generally conical in shape. The basal inner tooth may be apically rugose to distinctly spinose (Figs. 163, 165). It bears the slightly sinuate seta subdentalis in a cusp on its anterodorsal surface (Figs. 161- 176). The apical tooth (from the base of the distal inner tooth) to its apex is about one-fifth the length of the mandible and about 2.5 times as long as its basal width. Lateroventral seta S_1 is indistinct, S_2 and S_3 appear to be simple (Fig. 165). The A_1 /MD ratio is in the 2.0-3.0 range.

The maxilla is shown in Fig. 112. The lacinia (Lc) bears a fringe of lacinial chaetae (LCh). A distinct galea is not present. The stipes (St) bears two simple setae and a simple ring-like palpiger (Fig. 112). The basal paraxial seta is on a short membranous pedicel. The antaxial seta could not be seen. The maxillary palpus is one-segmented (Figs. 112-118) with an indistinct CS toward its apex (0.7-0.9 from base). The apical sensillae are as in Figs. 112, 117. P_b is two-segmented (Figs. 116-118) sensillae c and f are relatively short and sensillae d is large and apically membranous. P_1 is about 2.4-5.0 longer than its mesal width. A_1/P_1 varies from about 6.0 to 8.5.

The mentum is as in Figs. 123, 128. The M appendage (MApp) is indistinctly separated from the mentum. Lateral vesicles are present on each



FIGS. 18-45. Pupal RO: 18-29, *L. pilosella:* 18, allotype, *L. floridana* FL; 19, female paratype *L. floridana* FL; 20, Caster Creek, S.R.P. SC; 21, Savannah River, SC; 22, Mill Creek NC; 23, Mill Creek, NC; 24, Skootanaha River ONT; 25, Firehole River WY. 26-28, detail of ANi: 26, ex Fig. 21; 27, ex Fig. 24; 28, ex Fig. 25; 29, detail of base of RO. 30-34, *L. becki:* 30, Little Haw River FL; 31, Lake Lacawac PA; 32, Lake Lacawac PA. 33-34, detail of ANi: 33, ex Fig. 32; 34, ex Fig. 30. 35-45, *L. maculata:* 35, Nelson Res. KA; 36, Belew's Lake NC; 37, Short Creek KA; 38, Short Creek KA; 39, Belew's Lake NC; 40, Belew's Lake NC; 41, Nelson Reserve KA. 42-45, detail of ANi: 42, ex Fig. 39; 43, ex Fig. 38; 44, ex Fig. 37; 45, ex Fig. 41.

side of the Mapp. The pseudoradula consists of irregularly placed granules. In some specimens these tend to fade out apically (Fig. 129). The base of the pseudoradula generally ends bluntly in the plate below the submentum (Figs. 123-127) but in some cases (mostly in those species with head pustules and maculation (Figs. 107-111), appears to end in an ovoid shaped base between arms of the submental plate (Figs. 128-131). Two to three dorsomental teeth appear to be present. The ligula (Figs. 177-205) resembles that of *Nilotanypus* . The mesal tooth (M_t) is longer than (Figs. 189-197) or subequal to the outer tooth (Figs. 177-188). The inner tooth (I_t) is shorter than either the mesal or outer teeth. Apically the ligula is pale brown and the muscle scar is generally transversely ovoid. The paraligula is bifid (Figs. 178, 186) though an occasional partial trifid paraligula (Fig. 180) can be found and one species (Fig. 204) has three small outer teeth. The apex of the inner tooth is about 0.8 from the base of the paraligula. The lengths of the ligular teeth are measured as shown in Roback 1985, Fig. 86. The pecten hypopharyngis (Figs. 185, 188, 201) bears 6-10 moderately elongate teeth, only the innermost may be larger.

The anterior prolegs (AP) vary from about 370-480 μ in length and are furcate about 0.7 μ total length from the base (Figs. 285, 286). They are so extensile that accurate measurements are difficult. The apical claws of the AP are shown in Fig. 292. Those below 29 μ L generally have 2-3 apical teeth while the longer teeth are simple or with one small preapical tooth. The body bears only scattered simple setae. The procerci range from 93-229 μ in length and apically bear seven dark setae. These setae may vary from 450-700 μ in length. The anterodorsal and caudoventral setae of the procerci are simple (Fig. 287, 288). The procerci vary from about 3.3-8.8 times as long as wide. The degree of compression in mounting affects this ratio greatly. The posterior parapods are about 370-440 μ long and bear a distinctive subbasal (SBS) seta. This seta (Figs. 208-210, 218-221, 234-241, 245-247, 263, 273) may be relatively simple (Figs. 225-227, 260-263, 267, 268, 270) but in most cases bears 1-10 lateral spines in varying configurations (Figs. 218, 221, 234-241). The pattern and number of these lateral spines may in some cases be species specific but there is considerable variation in exact number within any species (Figs. 234-241). The subbasal seta varies from 130-207 μ in length. On each side of the SBS seta there is a small sensillum (?CS) about 5 μ in diameter (Fig. 291). These are not always clearly visible. The subbasal seta is generally about half as long as the posterior parapods. Apically each posterior parapod bears 13, generally pale-brown, claws. One of the smaller of these claws (PPCl) is bifid with the lower spur longer than the upper. Like the SBS setae the shape of this bifid claw may be species specific (Figs. 206, 207, 211-217, 228-233, 242-244, 264-266, 278-281). Also like the SBS seta there is considerable variation within any single species (Figs. 228-233, 264-266). The parameters of this bifid claw are measured as in Fig. 211 (A, B, C). Some species may have one or two darker heavier claws associated with this bifid claw (Figs. 269, 271) or a claw with fine inner and outer spinules (Fig. 284). The long thinner claws are finely pectinate (Fig. 289).

The anal tubules (4) are conical (Fig. 290) and range from about 160-290 μ in length and about 7 to 13 times as long as their greatest width. Generally they are about half as long as the posterior parapods. The supraanal setae are simple and about 290-380 μ long. They vary from 0.7-0.9 length of the posterior parapods. The lateral setae below the procerci and the supraanal setae are very small and difficult to discern. Many larval measurements, ratios and their means are given in Tables 1-5.

KEY TO PUPAL STAGE

1. Abdominal maculation with clear lacunae as in Fig. 77. . . . . .Trinidad. *L.* sp. 12

- Abdominal maculation with lacunae (Fig. 13), along caudal margin (Fig. 15) or absent (Fig.14)

.... 2

2. Respiratory atrium with elongate preapical groove (Figs. 59, 60, 62-64, 68); caudo-mesal groove variable (Figs. 59, 62, 68), RA may be wholly (Figs. 59, 62) or partially S-shaped (Fig. 68)................................ 3

- Respiratory atrium club-shaped (Figs. 18-25, 30-32), ovoid (Figs. 55,56,66) or wedge or hatchet-shaped (Figs. 35- 41).................... 5

3. Plastron plate large and distinct (Figs. 69,70); caudo-mesal groove small; RO about 142 µ L; AeT about 15 µ L (Fig. 70); S- shape of RA only suggested ....Trinidad *L.* sp. 11.

- Plastron plate small (Figs. 61, 65); caudo-mesal groove deep; RO over 240 µ L; AeT (Figs. 61, 65) over 34 µ L; RA distinctly S- shaped (Figs. 59, 60, 62- 64) 4

4. Respiratory organ as in Figs. 59,60; AL 385-392 µ L (Fig. 89); longest spinules of AL 29-31 µ L (Fig. 90).................... *L. virescens*

- Respiratory organ as in Figs. 62-64; AL 289-355 µ L (Fig. 91); longest spinules of AL 15-19m L (Fig. 92)................. *L.* sp. 3 nr. *virescens*

5. Respiratory organ >370 µ L as in Fig. 66; ANi (Fig. 67 robust; AeT alongate sinuate (Fig. 67), recurved on self .... *L.* sp. 10

- Respiratory organ <300 µ L; ANi shorter (Figs. 26,33,43,51, 57); AeT (Figs. 26,33,43,51,57) at most slightly sinuate, never recurved on self 6

6. Aeropyle tube 29-32 µ L (Figs, 51-53); generally lies along outer margin of RO (Figs. 46-54) .. 7

- Aeropyle tube <24 µ L (Figs. 26, 28, 33, 34, 42, 45, 57, 58); preapical groove of RA apparently absent (Figs. 57,58), shallow (Figs. 42-45) or very distinct (Figs. 26, 34); if preapical groove present, AeT inserted into upper margin of groove (Figs. 26, 34) 8

7. Respiratory organ 192-250 µ L (Figs. 46-50); AeT as in Figs. 51-53. S.E. United States .... *L. neopilosella*

- Respiratory organ 264m L (Fig. 54), Alaska... .... *neopilosella* var. 1

8. Respiratory organ very globose (Figs. 55, 56); preapical groove not evident; AeT more sinuate (Figs. 57, 58)............... *L. johannseni*

- Respiratory organ more triangular (Figs. 35-41), club-shaped (Figs. 18-25, 30-32) or hatched-shaped (Fig. 75); preapical groove very shallow (Figs. 42-45) or distinct (Figs. 26-28, 33, 34)..... 9

9. Preapical groove of RA very shallow (Figs. 43-45, 74); RO more triangular or hatchet-shaped (Figs. 35-41, 73, 75)....................10

- Preapical groove of RA very distinct (Figs. 18-25, 30-32); RO more club-shaped.............. .... *L. pilosella* , *L. becki*

10. Respiratory organ triangular or wedge-shaped (Figs 35-41); caudo-mesal indentation shallow (Fig. 35-41, 75)............... *L. maculata*

- Respiratory organ as in Fig. 73; caudo-mesal indentation deeper (Fig. 73) creating hatchet-shaped RA........ Venezuela ...... *L.* sp. 1

KEY TO LARVAL STAGE

1. Head completely pustulate (Figs. 104-111); LVS and CVS groups absent (Fig. 106); LVS group present (Figs. 104, 105) or LVS and CVS groups present (Figs. 107-111) 2

- Head non-pustulate (Figs. 95-103); LVS group generally present (Figs. 95-96, 101, 103) CVS group rarely present (Figs. 99, 100).........7

2. Head without ventro-mesal maculation (Fig. 104-106); small LVS group may be present (Figs. 104, 105); caudal margin often darkened (Fig. 106).. 3

- Head with faint to distinct ventro-mesal maculation (Figs. 107-111); LVS and CVS groups present.................................4

3. Head with small LVS group present (Figs. 104, 105); caudal margin not darkened; lower groove of bifid claw u-shaped (Figs. 206, 207) U.S. ....*L. maculata*

- Head without LVS group (Fig. 106): caudal margin maybe darkened (Fig. 106); lower groove of bifid claw forming acute angle (Figs. 211-217). U.S......................... *L. pilosella*

4. Head weakly marked (Fig. 107); IC about 0.50; LVS and CVS groups weak (Figs.107, 160): second small claw of PP with inner and outer spines (Fig. 284) upper spur of PPCl shorter (Fig. 284) Colombia.................. *L.* sp. 9

- Head more strongly marked (Figs. 108-111); spur groups, esp. CVS, stronger (Figs. 154-160); lower and upper spurs of PPCl subequal (Figs. 276-281) 5

5. A_2 >70 µ L; AR < 3.00; head with broadly quadrate maculation (Fig. 109); PPCl as in Fig. 276,

U.S. .... *L.* sp. 6

- A_2 <70μ; AR > 3.00; head with sinuate maculation (Figs. 108- 111) to more narrowly quadrate (Fig. 110); PPCl as in Figs. 278- 281 6

6. Head maculation as in Fig. 108; MD as in Fig. 173 without spur below inner teeth; PPCl as in Figs. 278-280, not highly arched overall. Colombia.. .... *L.* sp. 7
- Head maculation as in Figs. 110,111; MD with apparent spur below inner teeth (Figs. 175,176); PPCl as in Fig. 281, more highly arched overall. Cuba. .... *L.* sp. 8

7. PPCl with lower groove diagonally u-shaped (Figs. 228-233, 242, 244, 248, 250-252); B/C generally <1.00; M_t/0 of Li generally over 1.05 (Figs. 189-197) 8
- PPCl with lower spur elongate, lower groove forming more acute angle (Figs. 211-217, 222-224, 259,261-262, 264-266, 269, 271, 274); B / C generally >1.02. 12

8. Head with brown transverse band (Figs. 101-103); LVS group with 7-18 spurs (Fig. 151) ... . *L. johannseni*
- Head without maculation; LVS group with 6-30 spurs 9

9. LVS group with about 28 spines (Fig. 145); lower spur of bifid PP claw a short arc (Fig. 248); SBS seta base with elongate spines (Fig. 249) .... *L. neopilosella* var. 2.
- LVS group with <16 spines (Figs. 141-144, 146-148); bifid claw of PP as in Figs.228,242, 257; base of SBS seta more flag-like as in Figs. 239-241, 245-246, 258 or with long spines (Figs. 234-238, 247) 10

10. SBS seta with elongate spines along base (Figs. 234-241); lower groove in forked PPCl narrow and relatively parallel sided (Figs. 228- 233). .. .. *L. neopilosella*
- SBS seta with shorter spines, more flag-like (Figs. 245-247, 258; groove in PPCl wider and more open (Figs. 242-244, 257) 11

11. Caudal third of head may be faintly infuscated (Fig. 98); LVS group may have two longer spurs (Figs. 147, 148); forked claw of PP as in Figs. 242-244; base of SBS seta as in Figs. 245-247 . ... *L. neopilosella* var. 4.
- Head clear; LVS group reduced (Fig. 146); groove of forked PP claw forming a wide U (Fig. 257); base of SBS flag-like (Fig. 258). .... *L. neopilosella* var. 3

12. LVS group consists of a large single spur about 20μ L (Figs. 99-100, 150); a reduced CVS group present (Figs. 99, 100) .... *L.* sp. 4.
- LVS group of 2-7 small spines (Figs. 95, 139, 140, 152, 153); distinct CVS group absent (Fig. 95) 13

13. SBS seta with 6-7 spines in irregular arrangement (Figs. 272, 273); Pl with 3 fine outer spines (Fig. 204) Colombia .... *L.* sp. 5.
- SBS relatively simple, 1-3 fine lateral spines (Figs. 225- 227, 260, 263, 267, 270); Pl bifid (Figs. 198, 202, 205) 14

14. Lower spur of bifid PP claw short (Figs. 222-224); distance B (Fig. 211) 64-67μ, A_1, 163-170μ .... *L. becki*
- Lower spur of bifid PP claw elongate (Figs. 259, 261, 262, 264- 266, 271); distance B (Fig. 211) 76-110μ; A_1, 211- 306μ 15

15. MD <100μ L (Figs. 170); L_1 (Figs. 203, 205) <60 L_j; PP may have dark claw (Fig. 271) in addition to forked claw 16
- MD >100μL (Figs. 165, 169); Li (Figs. 198, 199, 202) >69μ L; PP without dark claw. U.S., Colombia 17

16. Pc 218μL; L/W 8.43; PP with dark claw (Fig. 271). Cuba .... *L.* sp. 1.
- Pc <171μ; L/W 6.33-7.67; additional heavier claw of PP not darker than PPCl . Colombia ... . *L.* sp. 2 nr. *virescens*

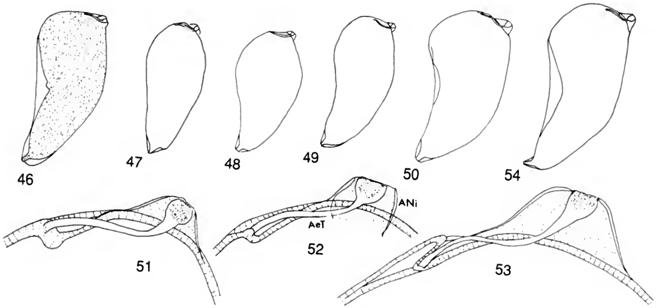
17. A_1 252-306μ; A_1/P_1 7.29-7.51. U.S. .... *L. virescens*
- A_1 237-244μ; A_1/P_1 6.51-7.09. Colombia ... . *L.* sp.1 nr. *virescens*

Labrundinia pilosella group

PUPA. RO club-shaped (Figs. 18-25); distinct preapical groove (Figs. 18-28).

LARVA. Head with or without pustules (Figs. 95, 106); LVS group on head indistinct to present (Figs. 95, 106, 139); CVS group absent on head (Figs. 95, 106); no maculation on head; SBS seta with 2-5 small lateral spinules (Figs. 218-221, 225- 227); lower spur of bifid claw parallel to base and relatively short (Figs. 211-217, 222-224); B/C (mean) 1.056-1.172

SPECIES. *L. pilosella*, *L. becki*



FIGS. 46-54. Pupal RO: 46-53, *L. neopilosella:* 46, Jocassee Res. NC; 47, paratype FL; 48, paratype FL; 49, Millrock Branch GA; 56, Mill Creek NC. 51-52, detail ANi: 51, ex Fig. 46; 52, ex Fig. 49; 53, ex Fig. 50; 54, *L. neopilosella* var. 1, AK.

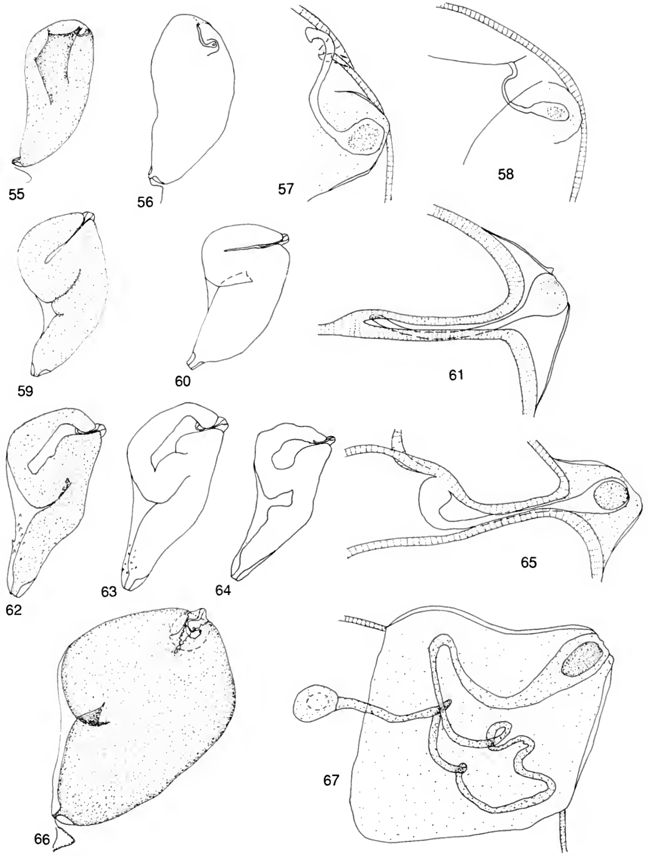
Distribution. Widespread U.S., Canada, Trinidad, Venezuela This appears to be primarily a North American group, which on the basis of some pupae collected by Dr. Coffman extends into the Neotropical Region. The placement of the PEx from Trinidad and Venezuela into L. pilosella is tentative. The pupae of *L. pilosella* and *L. becki*, unlike the larvae, are not readily separable. The RA preapical groove of the Neotropical PEx are deeper and more like those of *L. pilosella* (Figs. 26-28). *L. pilosella* is widespread over the entire U.S. and Canada while *L. becki* appears to be chiefly southeastern U.S.

Labrundinia pilosella (Loew).

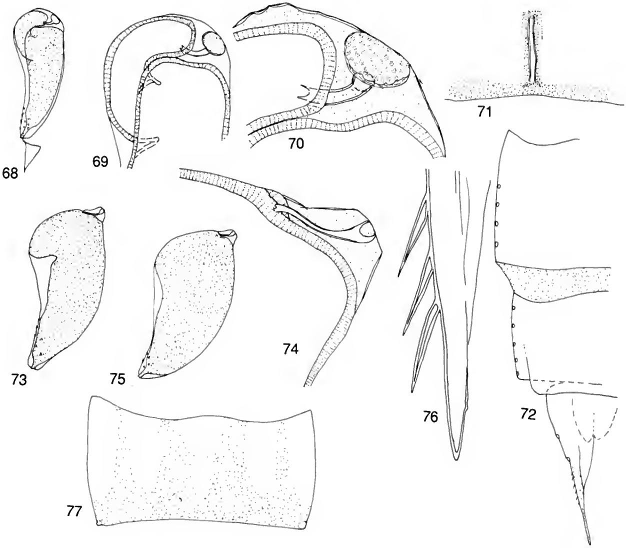
Tanypus pilosellus Loew 1866: 5,6
Labrundinia floridana Beck & Beck 1966: 339.
Labrundinia pilosella: Roback 1971: 276.
nec.*Labrundinia pilosella* Fittkau & Murray 1986: 85, Figs. 5.20, A, D-I.

This is the most ubiquitous of the included *Labrundinia* species— ranging from Maine to California and the Canadian Northwest Territories to Florida. Its southernmost distribution limit is at present, unknown as we have few collections from Mexico, Honduras or Guatemala. The larva is distinguished by its pustulate head (Fig. 106), the lack of LVS or CVS groups on the head and the form of the furcate PP claw. The pupal RO has a moderately deep preapical groove in the RA (Figs. 18-25) and a short AeT (Figs. 26-28, Table 6). The pupa is not readily separable from that of *L. becki*. There is considerable variation in the pupal RO (Figs. 18-25) and the larval PP bifurcate claw Figs. 211-217) but with the few rearings available, subspecific groupings are not possible at present.

PUPA. FA as in Fig. 6; RO with preapical groove, variation as in Figs. 18-25; spines at base of RO in Fig. 29; detail of ANi and enclosed AeT shown in Figs. 26-28; thoracic comb as in Fig. 4; detail of furcate Dcs1 (Fig. 10); Dcs2 in Fig. 11: WP clear to pale brown; abdominal tergites pale brown to clearly brown patterned as in Fig. 13; setae of A.IV arranged as in Fig. 13; detail of D_1, D_3 and D_4 of A.IV in Figs. 7-9; arrangement of LS, VII, VIII and AL shown in Fig. 78; detail of



FIGS. 55-67. Pupal RO: 55-58, *L. johannseni:* 55, Rayonier Ditch FL; 56, holotype. 57-58, detail ANi: 57, ex Fig. 56; 58, ex Fig. 55. 59-61, *L. virescens:* 59, holotype; 60, paratype; 61. detail ANi ex Fig. 60. 62-65, *L.* sp. 3 nr. *virescens*: 62-65, Belew's Lake NC: 65, detail ANi ex Fig. 63; 66, *L.* sp 10; 67, detail ANi ex Fig. 66.



FIGS. 68-77. Pupa. 68-72, *L.* sp. 11: 68, RO; 69, apex of RO; 70, detail of ANi; 71, scar A.I; 72, A.VII, VIII and AL. 73-74, *L.* sp. 1: 73, RO; 74, detail of ANi; 75, *L. maculata,* RO, Trindad; 76, *L.* sp. 3, detail apex of AL; 77, *L.* sp. 12, color pattern A.IV.

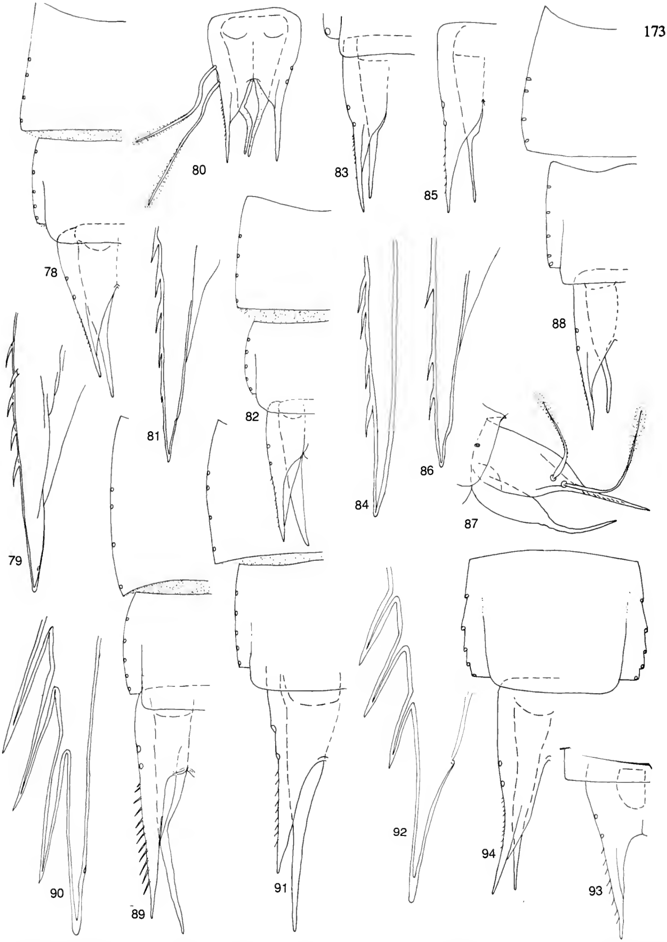
apex of AL as in Fig. 79; other characters and measurements given in Table 6.

LARVA. Head (Fig. 106) wholly pustulate about 432μ L; distinct LVS or CVS groups lacking; head may be wholly clear to caudal 0.25 brown (Fig. 106); labrum as in Fig. 119; entire mentum and M appendage (MApp) shown in Fig. 123; base of Pr (Fig. 123); apex of MD in Fig. 161; P$_1$ similar to Fig. 118; Li, Pl and PH shown in Figs. 177-179; variation in one pair of Pl in Fig. 180; AP similar to Fig. 285; claws of AP from smallest to largest in Fig. 292; SBS with 2-5 spinules near base (Figs. 218-211); the variation in the PPCl is shown in Figs. 211-217; measurements of claw used in tables are taken as in Fig. 211; other characters and measurements given in Table 1.

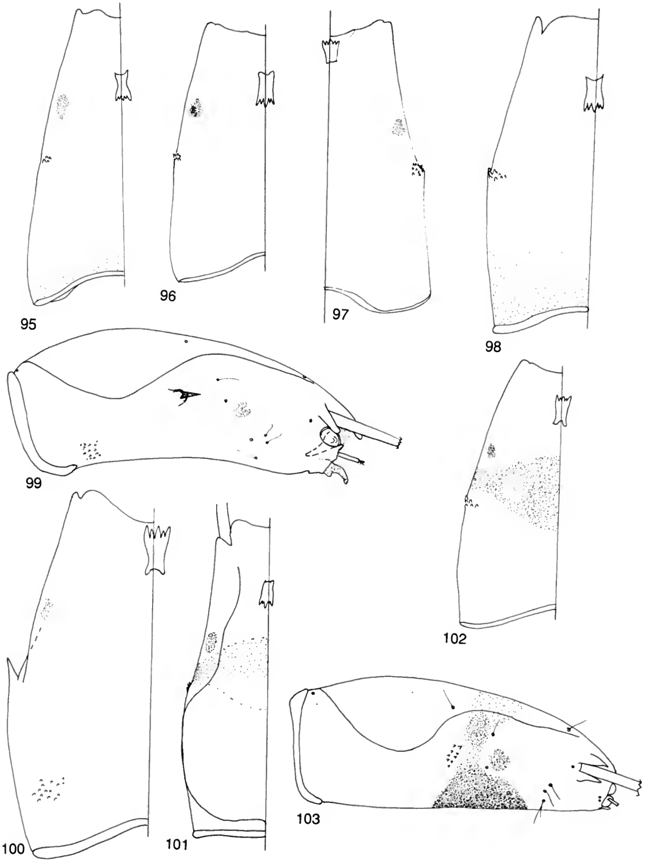
SPECIMENS EXAMINED. CANADA: **NORTHWEST TERRITORIES:** La (III) Harris River, 20-IX-1971, coll. Wiens & Crocher [CNC]; 6mA, Harris River, 61/52N, 121/19W [CNC]; 2La (III), 2mA, Martin River [CNC]; 2La, 1 La (III), Martin River, 18-IX-1971, coll. Crocker and Wiens [CNC]; La (III), Martin River, 14-IX-1972, pipeline project [CNC];

La (III), Martin River, 29-XI-1972, pipeline project [CNC]; fLa, PEx, A, Martin River, 31-VII-1973, pipeline project [CNC]; 3fLa, PEx, A, Martin River, 1-5-VI-1973, coll. Collins [CNC]; 6La (III), 3 La (II), Trail River, 7-IX-1972, pipeline project [CNC]. **ONTARIO :** La, St. Lawrence River, ENE Tremont Isl., 14-VII-1976, coll. Oliver & Tinker [CNC]; La, Lake St. Clair, 24-VII-1963, coll. Hiltunen [CNC]; fPEx, Skootanaha River, 27-VII-1974, coll. Coffman [COFF]; mA, Canagagigue River, Waterloo, 14-VIII-1975, coll. Bilyj [CNC]; mPEx, same locality 18-VIII-1975 [CNC]; La, mA, 2fA, same locality 24-X-1975 [CNC]; mPEx, same locality, 17-19-VIII-1976 [CNC]. **QUEBEC :** La, L. Matamec, 5-X-1977, coll. Kreamer [CNC]; La, same locality, 26-V-1978 [CNC].

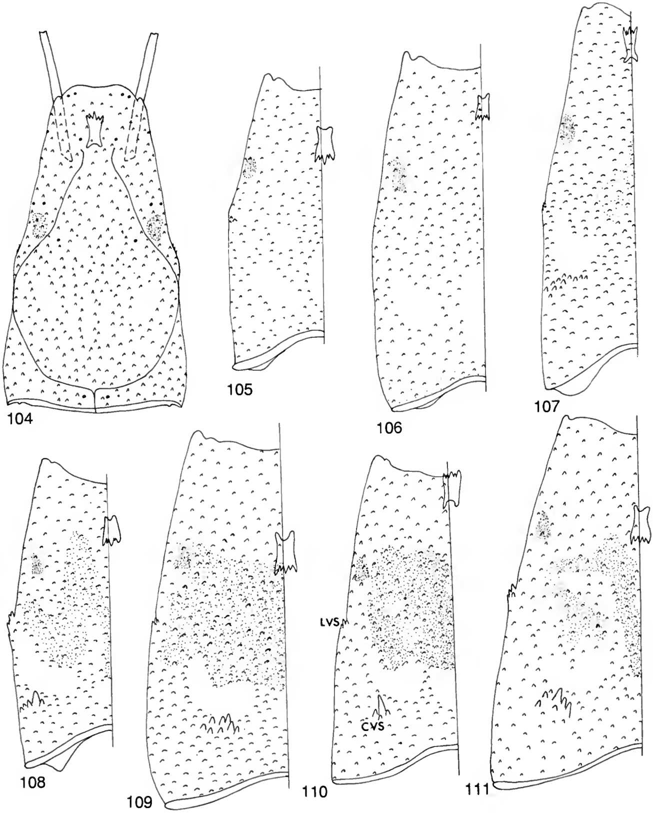
UNITED STATES: **CALIFORNIA :** 3La, Refugio Creek, Sta. Barbara Co., VII-VIII-1973, coll. Hart [ANSP]. **FLORIDA :** La, Small Creek, Fla. 315, Merion Co., 17-III-1952, coll. Beck [ANSP]; La, Ochlocknee River, Fla. 12, Leon Co., 7-IX-1961, coll. Beck [ANSP]; La, Suwannee River, Suw. springs, Suwannee Co., 3-II-1953, coll. Beck [ANSP]; La, same river, Lafayette Co., 21-VII-1955, coll. Beck [ANSP]; La, Istokpoga Creek, U.S. 90, Highlands Co., 12-XI-1958, coll. Beck [ANSP]; La, Kissimmee River, U.S. 98, Highlands Co., 5-V-1961, coll. Beck [ANSP]; La, Mosquito Creek, U.S. 90, Gadsden Co., 30-XI-1960, coll. Beck [ANSP]; La, Chipola River, Fla. 20, Calhoun Co., 12-IV-1972, coll. Carlson [ANSP]; La, Hillsboro River, U.S. 301, Hillsboro Co., 3-V-1961, coll. Beck [ANSP]; La, Horse Creek, De Soto Co., 13-IV-1978, coll. Rutter [FDER]; La, Shell Creek, Charlotte Co., 7-VI-1976, coll. Rutter [FDER]; La, Fisheating Creek, Glades Co., 23-IX-1983, coll. Rutter [FDER]; 2La, St. Mark's River., Natural Bridge Park (79), 8-VI-1972, coll. Roback [ANSP]; mLa,PEx; fLa, PEx, A, Little Horse Creek, Flagler Co., 21-III-1964, coll. Beck [FLSM]; fLa, PEx, A, Porters Creek, Clay Co., 21-II-1963, coll.Beck [FLSM]; mLa,PEx,A, same locality, 7-III-1963, coll. Beck, [USNM Holotype 69123, *L. floridana*]; fLa, PEx, A, same data [USNM, Allotype 69123, *L. floridana*] fLa, PEx, A, Rayonier Ditch, Flagler Co., 23-X-1963, coll. Beck [ANSP, paratype *L. floridana*]. **GEORGIA :** mPEx,A, Kinchafoonee Creek (65) nr. Preston, 25-V-1972, coll. Roback [ANSP]; La, fP, Gum Creek nr. Cordele, Crisp Co., 31-X-1983, coll. Richardson [ANSP]; 2La, Gum Creek nr. Cordele, (66) 26-V-1972, coll. Roback [ANSP]; La, Satilla River (92) S.E. Waycross, 24-VI-1972, coll. Roback [ANSP]; mLa,PEx, fLa,PEx,A, Ochlocknee River at U.S. 84, Thomas Co., 9-X-1986, coll. Caldwell & Stevens [GDNR]; mPEx,A, Ochlocknee River, FAS 1943, Colquitt Co., 18-IX-1984, coll. Caldwell [GDNR]; mPEx, Estanolle Creek at Hwy 17, Stephens Co., 18-VIII-1981, coll. Caldwell [GDNR]; mPEx, A, Kings Gap Creek nr. Pine Mt., Harris Co., 2-V-1985, coll. Caldwell [GDNR]; PrP, 3mP, Savannah River above Lock & Dam, Augusta Richmond Co., 16-X-1973, coll. Peterson, Hodges, Kennedy [GDNR]. La, Savannah River at Rt 301, Screven Co., 26-IX-1973, coll. Caldwell & Walker [GDNR]; La, PrP, Flint River (Lake Seminole) at Buoy 179, Decatur Co., 24-VIII-1971, coll. Hall & Gaddis [GDNR]; La, mP, Chattooga Creek, 1.0 mi. W. Ridgeway Church, Chattooga Co., 28-VIII-1974, coll. Caldwell & Petersen [GDNR]; -La, Potato Creek, Calvary Church Rd., Lamar Co., 26-IX-1979, coll. Gaddis & Sloope [GDNR]; La, Withlacoochee River at GA 31, Lowndes Co., 3-XI-1974, coll. Caldwell & Petersen [GDNR]; La, Suwannee River nr. GA 177, Clinch Co., 19-X-1972, coll. Caldwell & Gaddis [GDNR]. La, Oconee River at State Rd. 1086, Clark-Oconee Cos., 24-VIII-1971, coll. Caldwell & Walker [GDNR]; fPEx, Indian Creek at Locust Grove Rd., Henry Co., 16-IX-1981, coll. Caldwell & Laquidara [GDNR]; -fPEx, Tom's Creek at Mc Curley Rd., Franklin Co., 26-VIII-1981, coll. Caldwell & Farrell [GDNR]; La, Big Creek (68) S.W. Hawkinsville, Rt. 27 E., 28-V-1972, coll. Roback [ANSP]. **ILLINOIS :** La, Ditch, tributary of Long Point Slough, Illicpolis, 25-IX-1984, [ANSP]. **KANSAS :** La, Maria des Cygnes River, N. of Rantout, Franklin Co., 8-X-1981, coll. Bilyj [WINN]; La, mfPEx, Plum Creek, S.E. of Kickapoo, Leavenworth Co., 22-VII-1981, coll. Ferrington [KA]; 3mPEx, Coal Creek, N.W. of Niles, Ottawa Co., 7-X-1980, coll. Ferrington [KA]. **KENTUCKY:** La, Green River, N.W. of Birk City, 6-VIII-1981, coll. Richardson [ANSP]. **MAINE:** La, Webster Brook, Aroostook Co., 16-IX-1981, [ANSP] La, Greenlaw Stream, Aroostook Co., 14-IX-1981, [ANSP] **NEBRASKA:** 2La, Lost Creek nr. Schuyler, Colfax Co., 5-VII-1984, coll. Bazata [NEBR]; 2La, Loup River, Fullerton, Nance Co., 20-IX-1972, coll. Bazata [NEBR]. **NEW HAMPSHIRE:** 2fPEx, Androscoggin River nr. Rt. 16, 21-VII-1981, coll. Coffman [COFF]. **NEW YORK:** m3fPEx, Lake Champlain, Westport, 11-VIII-1984, coll. Coffman [COFF]; 3m PEx, Bouquet River, Essex Co., 10-VIII-1984, coll.



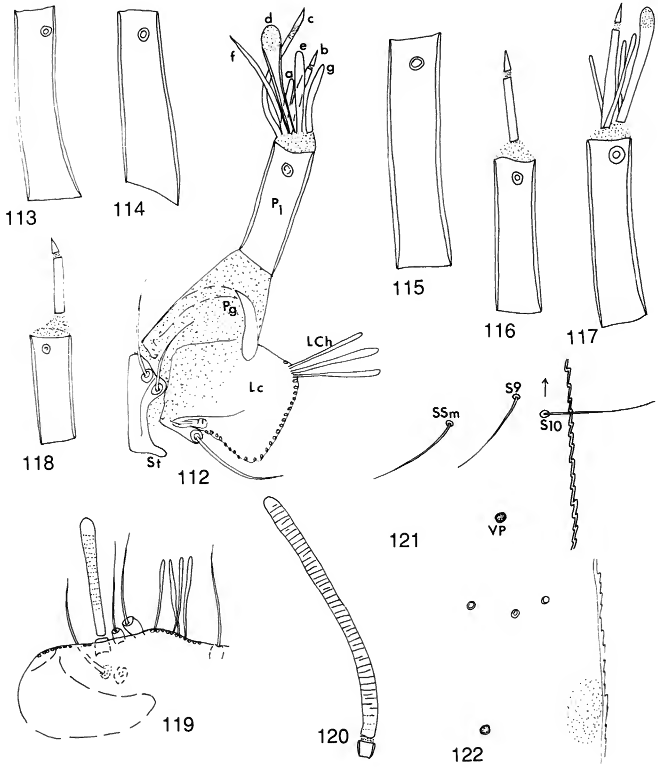
FIGS. 78-94. Pupa. 78, *L. pilosella* male A.VII, VIII and AL; 79, *L. pilosella* detail tip of AL; 80, *L. maculata* male AL and LS. AL; 81, *L. maculata* detail tip of AL; 82, *L. becki* male A.VII, VIII and AL; 83, *L. neopilosella* male AL; 86, *L. neopilosella* var. 1, detail apex of AL; 87, *L. neopilosella*, male AL, LS, and male GS, lateral; 88, *L. johannseni*, male A.VII, VIII and AL; 89, *L. virescens* male holotype, A.VII, VIII and AL; 90, *L. virescens*, detail of apex of AL; 91, *L.* sp. 3 nr. *virescens*, male A.VII, VIII and AL; 92, *L.* sp. 3 nr. *virescens*, detail apex of AL; 93, *L.* sp. 3. nr. *virescens*, female AL; 94, *L.* sp. 10, male A.VIII and AL.



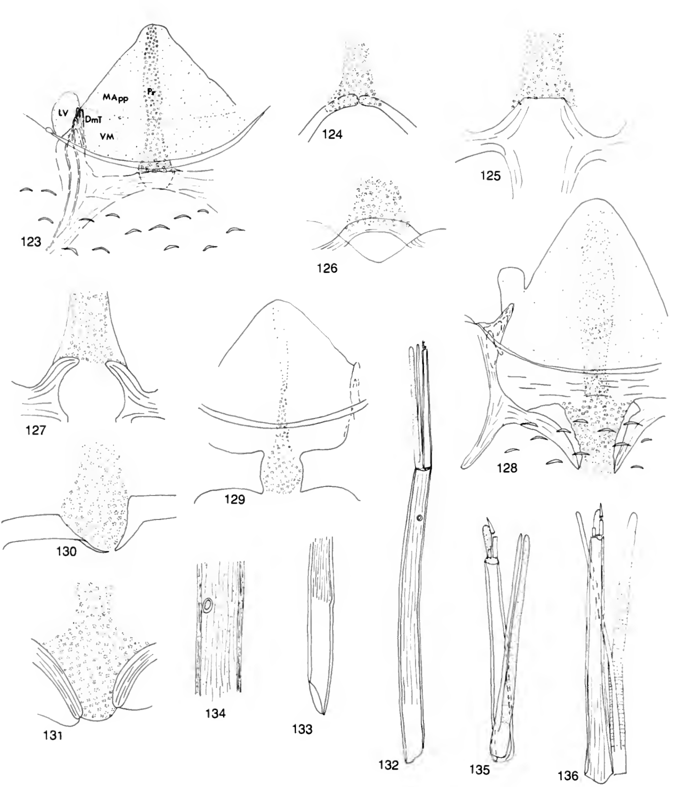
FIGS. 95-103. Larval head: 95, *L. becki,* ventral; ,96, *L. neopilosella,* Whitney NC, ventral; 97, *L. neopilosella,* Bays Mt. Lake, TN, ventral; 98, *L. neopilosella* var. 4, ventral; 99, *L.* sp. 4, lateral; 100, *L.* sp. 4, ventral. 101-103, *L. johannseni:* 101, dorsal; 102, ventral; 103, lateral.



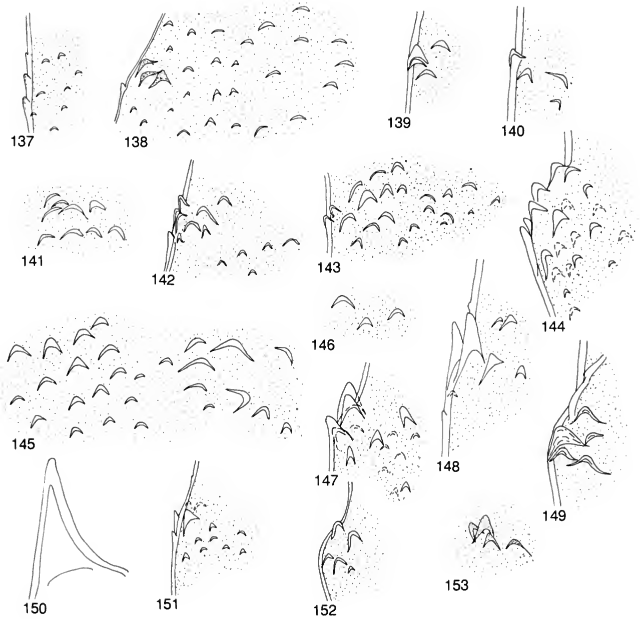
FIGS. 104-111. Larval head: 104, *L. maculata* KA, dorsal; 105, *L. maculata*, MEX, ventral; 106, *L. pilosella*, ventral; 107, *L.* sp. 9, ventral; 108, *L.* sp. 7, ventral; 109, *L.* sp. 6, ventral; 110, *L.* sp. 8, ventral; 111, *L.* sp. 8, ventral.



FIGS. 112-122. larva: 112, *L. becki*, entire palpus; 113-118, P1: 113, *L.* sp. 6; 114, *L.* sp. 8; 115, *L. virescens;* 116, *L. neopilosella*, with P_b; 117, *L.* sp. 4, with apical sensillae; 118, *L. maculata* with P_b; 119, *L. becki*, labrum; 120, *L. virescens*, detail of labral sensillum d; 120, lateroventral head setae, *L.* sp. 7; 121, lateroventral head setae, *L. maculata*.

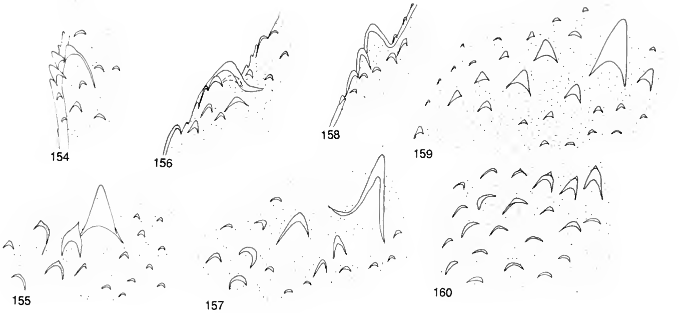


FIGS. 123-136. Larva. 123-132, mentum: 123, *L. pilosella*; 124, *L.* sp. 4, base of Pr; 125, *L.* sp. 2 nr. *virescens*, base of Pr; 126, *L.* sp. 9, base of Pr; 127, *L.* sp. 1, base of Pr; 128, *L.* sp. 7, entire; 129, *L.* sp. 3, base of Pr; 130, *L.* sp. 8, base of Pr; 121, *L.* sp. 6, base of Pr. 132-136, antenna: 132, *L. neopilosella* var. 2, entire; 133, *L.* sp. 7, detail of base of A_1; 134, *L. becki*, detail CS, A_1; 135, *L.* sp. 7, detail A_{2-4}, Bl and ABl; 136, *L. maculata*, detail A_{2-4}, Bl, ABl.



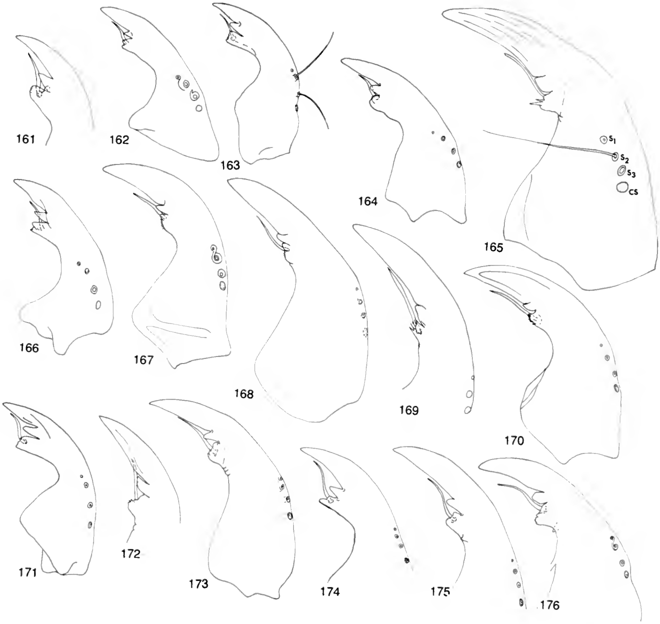
FIGS. 137-153. Larva, LVS head group: 137, *L. maculata* KA: 138, *L. maculata* MEX: 139, *L. becki*, Polk Cr. FL; 140, *L. becki*, VA; 141-144, *L. neopilosella:* 141, holotype; 142, paratype; 143, Rayonier For., FL; 144, Bays Mt. Lake TN; 145, *L. neopilosella* var. 2; 146, *L. neopilosella* var. 3; 147, *L. neopilosella* var. 4, Boliek's Pond FL; 148, *L. neopilosella* var. 4, Pond #28 KY; 149, *L. virescens*; 150, *L.* sp. 4; 151, *L. johannseni*; 152, *L.* sp. 1 nr. *virescens*; 153, *L.* sp. 2.

Coffman [COFF]. NORTH CAROLINA : La, White Oak River, Onslow Co., VII-1984, coll. Lenat [NC]; La, Trent River, Jones Co., VII-1980, coll. Lenat [NC]; -La, Avent Creek, Harnett Co., III-1981, coll. Lenat [NC]; PrP, Lumber River, Robeson Co., VII-1985, coll. Lenat [NC]; La, New Mill Creek, Onslow Co., VIII-1985, coll. Lenat [NC]; La, Fishing Creek, Halifax Co., VII-1985, coll. Lenat [NC]; La, Drowning Creek, Richmond Co., IX-1985, coll. Lenat [NC] -PrP, Lumber River, Robeson Co., X-1985, coll. Lenat [NC] -2La, Cape Fear River, Cumberland Co., I-1986, coll. Lenat [NC]; 2La, Tar River, Pitt Co., XI-1985, coll. Lenat [NC]; La, Maxwell Creek, Duplin Co., VI-1985, coll. Lenat [NC]; La, So. Frk. New River, Alleghany Co., V-1985, coll. Lenat [NC]; La, Nense River, Wake Co., VII-1983, coll. Lenat [NC]; PrP, Carvers Creek, Bladen Co., I-1983, coll. Lenat [NC]; La, Hunting Creek, Iredell Co., VIII-1983, coll.



FIGS. 154-160. Larva, LVS and /or CVS head groups: 154, *L.* sp. 6, LVS; 155, *L.* sp. 6, CVS; 156. *L.* sp. 7, LVS; 157, *L.* sp. 7, CVS; 158, *L.* sp. 8, LVS; 159, *L.* sp. 8, CVS; 160, *L.* sp. 9, CVS.

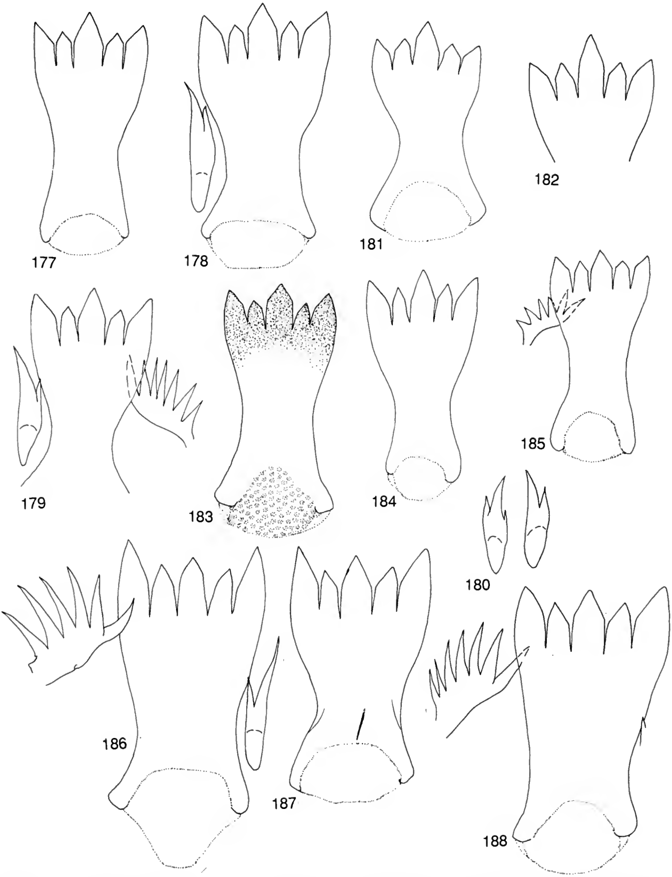
Lenat [NC]; La, Shalotte River, Brunswick Co., VII-1983, coll. Lenat [NC]; La, Broad River, Rutherford Co., VIII-1983, coll. Lenat [NC]; 2La, New River, Onslow Co., VII-1984, coll. Lenat [NC]; La, Black River, Sampson Co., XII-1984, coll. Lenat [NC]; PrP, McLendons Creek, Moore Co., IX-1984, coll. Lenat [NC]; La, Barnes Creek, Montgomery Co., X-1984, coll. Lenat [NC] La, Smith Creek, Granville Co., XII-1984, coll. Lenat [NC]; La, Dutch Second Creek, Rowan Co., X-1984, coll. Lenat [NC]; La, Crabtree Creek, Wake Co., IX-1984, coll. Lenat [NC] La Maiden Creek, Catawba Co., IX-1984, coll. Lenat [NC]; 3fm, 2f PEx, Mill Creek, 22-X-1976, coll. Coffman [COFF]; La, Cape Fear River, 3 mi. S.W. Slocumb, Cumberland Co., 19-IX-1969, coll. Roback [ANSP]; La, Cape Fear River, 1 mi. S. Tolar Landing, Bladen Co., 16-IX-1969, coll. Roback [ANSP]. **PENNSYLVANIA:** La, Susquehanna River, 2 mi. E. of Meshoppen, 30-VIII-1983, coll. Richardson [ANSP]; mPEx, Linesville Creek, nr. Linesville, 11-V-1971, coll. Coffman [COFF]; mf PEx, Linesville Creek, nr. Linesville, 22-VII-1970, coll. Coffman. [COFF]. **SOUTH CAROLINA:** La, PEx, Wateree River, nr. Camden, 31-VIII-1958, coll. Roback [ANSP]; La, Edisto River, nr. Orangeburg, Rt 63 Bridge, 21-VII-1964, coll. Roback [ANSP]; La, Lower Three Runs, at Tabernacle Creek Rd., Allendale Co., 26-IX-1965, coll. Roback [ANSP]; 2f PEx, Caster Creek, Rt #3, Savannah River Plant, Barnwell Co., 23-III-1977, Coll. Roback [ANSP]; -La, Buck Creek, Horry Co., 4-I-1979, coll. White [ANSP]; La, Buck Creek, Horry Co., 30-X-1976, coll. Carlson [ANSP]; La, Simpson Creek, SC 905, Horry Co., 4-I-1979, coll. White [ANSP]; La, Little Garvin Creek, Anderson Co., 14-VII-1979, coll. White [ANSP]; La, Big Garvin Creek, Anderson Co., 16-I-1979, coll. White [ANSP]; La, Mountain Creek, at S-4-158, Anderson Co., 14-IX-1975, coll. Carlson [ANSP]; La. Sawara Branch, at S-32-104, Lexington Co., 28-XI-1976, coll. Carlson & White [ANSP]; La, Fishepoo River, nr. Wellsboro, Colleton Co., 4-II-1977, coll. Carlson & White [ANSP]; Little Bees Creek, S-27-69, Jasper Co., 4-II-1977, coll. Carlson & White[ANSP]. **SOUTH CAROLINA - GEORGIA** : f P, Savannah River, S. of Augusta, above Lock & Dam, 3-X-1964, coll. Roback [ANSP]; La, mPEx, Savannah River, mi. 175, about 7.5 mi. NE. Shell Bluff Landing, Aiken Co., SC-Burke Co., GA, XII-1961, coll. Roback [ANSP]; La, Savannah River, mi. 157, Brigham's Landing, Barnwell Co., SC, Burke Co., GA, 28-VIII-1968, coll. Richardson [ANSP]; same locality; La, mP, 18-IX-1972, coll. Roback [ANSP]; La, fP, Savan-



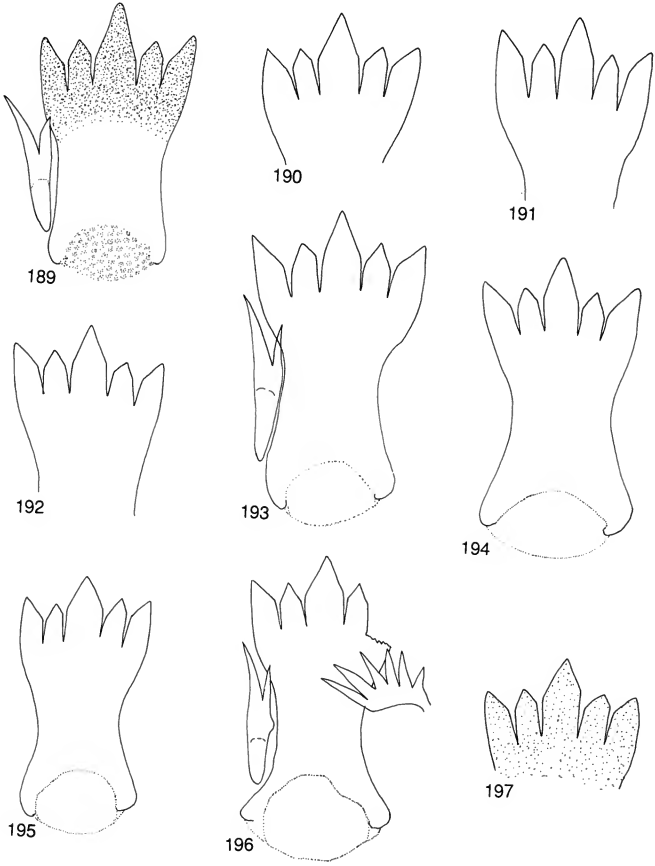
FIGS. 161-176. Larva mandible, ventral: 161, *L. pilosella,* apex; 162, *L. maculata;* ,163, *L. becki;* 164, *L. neopilosella,* holo.; 165, *L. virescens,* para.; 166, *L. johannseni;* 167, *L.* sp. 4. Belew's Lake NC; 168, *L.* sp. 4, Cooper River, NC; 169, *L.* sp. 1 nr. *virescens*, apex; 170, *L.* sp. 2 nr. *virescens*; 171, *L.* sp. 5; 172, *L.* sp. 6, apex; 173, *L.* sp. 7; 174, *L.* sp. 9, apex; 175, *L.* sp. 8, apex; 176, *L.* sp. 8, apex.

nah River, mi. 149, 1.5 mi. N. of Little Hell's Landing, Allendale Co. SC, Burke Co., GA, 29-VIII-1968, coll. Richardson [ANSP]; same locality fPEx, 10-IX-1980, coll. Roback [ANSP]; La, Savannah River (57) mi. 134, 1.25 mi. below Johnson's Landing, Allendale Co., SC, Screven Co., -GA, 21-VIII-1955, coll. Roback [ANSP]; same locality, 4La, 3PrP, mP, 8-VII-1971, coll. Roback [ANSP]; same locality, La, 19-VI-1984, coll. Richarson [ANSP]. **VIRGINIA** : PrP, Copper Creek, Scott Co., 2-VIII-1981, coll. Watson [WAT]; La, Potomac River, below confluence with Monocacy, 20-VIII-1961, coll. Roback [ANSP]. **TENNESSEE:** mPEx, Ecology Pond, Bays Mt. Lake, 30-V-1985, coll. Watson [WAT]; La, Tennessee River (Kentucky Lake) nr. New Johnsonville, 7-X-1958, coll. Roback [ANSP]. **TEXAS:** La, Beech Creek, Jasper Co., 24-XII-1981, coll. Bass [ANSP]. **WYOMING** : m,fPEx, Firehole River, Yellowstone Nat. Park, 21-VII-1975, coll. Coffman [COFF].

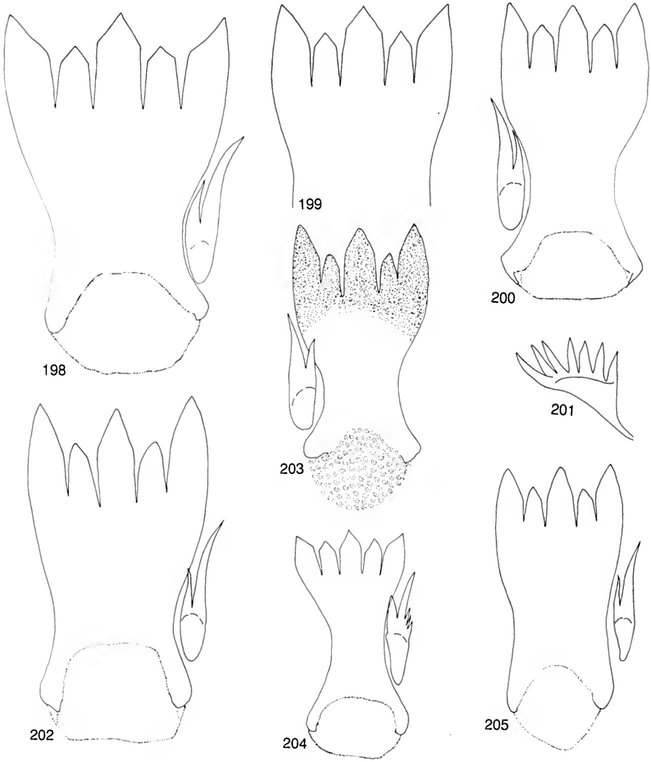
TRINIDAD: fPEx, Oropuche River, 15-I-1977,



FIGS. 177-188. Larval ligula. 177-180, *L. pilosella:* 177, Illiopolis, IL; 178, paratype *L. floridana* with Pl; 179, Savannah River SC, with Pl and PH; 180, Pl variation, Susq. Riv. PA; 181, 182, *L. maculata*; 181, Short Creek KA; 182, MEX, apex; 183, *L.* sp. 9. 184-185, *L. becki:* 184, Dismal Swamp, VA; 185, Polk Creek, FL with PH; 186, *L.* sp. 6 with Pl and PH; 187, *L.* sp. 7; 188, *L.* sp. 8 with PH.



FIGS. 189-197. Larval ligula. 189-191, *L. neopilosella:* 189, paratype; 190, apex from PA; 191, apex from PA. 192-193, *L. neopilosella* var. 4; 192, Pond #25 KY; 193, Boliek's Pond, FL with Pl; 194, *L. neopilosella* var. 3. 195-196, *L. johannseni:* 195 Nense River NC; 196, holotype with Pl and PH; 197, *L. neopilosella* var. 2, apex.



FIGS. 198-205. Larval ligula. 198-199, *L. virescens:* 198, holotype; 199, allotype apex; 200, *L.* sp. 4 with Pl; 201, *L.* sp. 4, PH; 202, *L.* sp. 1 nr. *virescens* with Pl; 203, *L.* sp. 2 nr. *virescens* with Pl; 204, *L.* sp. 5 with Pl; 205, *L.* sp. 1 with Pl.

Table 1. Comparison of range of measurements (μ) and ratios for larvae of the *L. pilosella* and *L. maculata* groups. Numbers in [ ] = n for means. A = absent, P = present.

	L. pilosella [10]		L. becki [6]		L. maculata [6]	
	r	mean	r	mean	r	mean
H-pustules	-P	-	-A	-	-P	-
H-Mac.C	0-0.25	-	0.25	-	-A	-
H-Mac. V	-A	-	-A	-	-A	-
H-LVS	-A	-	3-4	3.5[2]	3-5	4.0[5]
H-CVS	-A	-	-A	-	-A	-
A_1-L	170-215	186.9[9]	163-170	164.5	151-178	165.2
A_2-L	62-74	67.4[8]	70-79	74.5	66-74	68.5
AR	2.18-2.65	2.441[8]	1.87-2.10	2.006	2.04-2.28	2.165
MD-L	66-81	73	63-69	66.3	66-70	68
ApT-L/W	2.00-2.40	2.083[6]	2.00-2.25	2.083	1.78-1086	1.810[4]
ApT/MD	0.18-0.24	0.204[5]	0.17-0.20	0.183[4]	0.18-0.20	0.181[4]
A_1/MD	2.46-2.67	2.570[9]	2.36-2.70	2.482	2.16-2.62	2.408
P_1L	22-26	24	22-25	22.8[4]	19-22	21.3[4]
P_1L/W	2.43-3.60	3.203	2.83-3.00	2.958[4]	2.60-3.00	2.900[4]
CS.P_1	0.75-.088	0.817[6]	0.80-0.82	0.810[2]	0.73-0.87	0.793[4]
A_1/ P_1	7.40-8.27	7.756[9]	6.52-7.50	7.245[4]	7.45-8.09	7.850[4]
Li-L(O)	45-61	51.3	45-51	47	39-44	41.4[5]
It/O	0.95-0.98	0.968	0.95-0.99	0.967	0.97-1.00	0.990[5]
Mt/O	1.02-1.06	1.039[9]	1.02-1.06	1.043	1.08-1.15	1.124[5]
Pl-L	23-28	25.2[9]	22-25	23.3[3]	26-26	26.0[3]
no. teeth PH	7	-	6	-	-10	-
Pc-L	93-111	104.1[8]	111-130	121.4[5]	100-118	108.0[5]
PC-L/W	3.33-4.46	3.977[8]	4.38-5.00	4.642[5]	3.60-4.59	4.120[5]
PPCl-A	47-55	50.6	44-47	45.0[3]	39-48	43.4[5]
PPCl-B	70-95	81.8	64-67	65.7[3]	54-66	59.4[5]
PPCl-C	60-76	69.8	61-64	62.6[3]	66-73	67.4[5]
B/C	1.1-1.3	1.172	1.03-1.06	1.056[3]	0.86-0.90	0.881[5]
access dk. cl.	-A	-	-A	-	-A	-

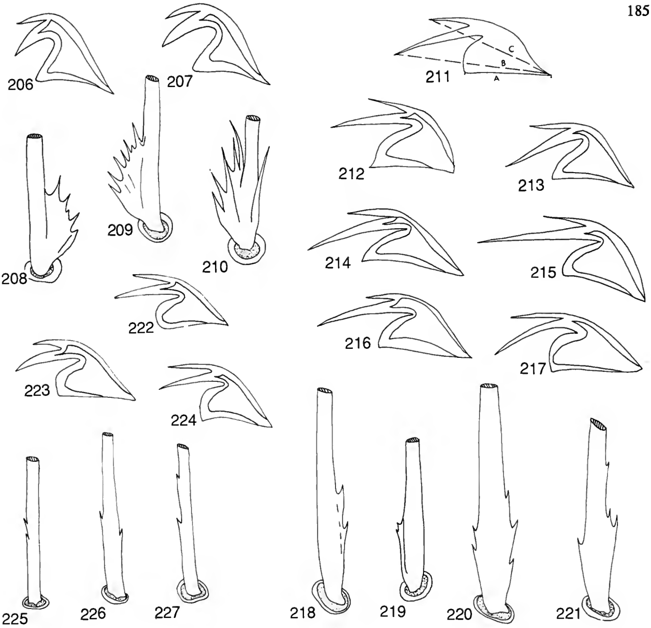
coll. Coffman [COFF].

VENEZUELA: mPEx, El Limon, 27-VI-1974, coll. Coffman [COFF].

Labrundinia becki Roback

Labrundinia becki Roback 1971: 279.
Labrundinia pilosella Beck and Beck 1966: 340.

This species is in most aspects closely related to *L. pilosella*. The larval head maculation (Fig. 95) and PPCl (Figs. 222, 223) are identical to those of *L. pilosella*. The head however lacks the overall pustules of that species. A distinct LVS group is present (Figs. 139,140). From the few pupae (Figs. 30-32) of *L. becki* available I have not been able to find a clear character to separate it from the pupa of *L. pilosella* (Figs. 18-25). Perhaps when larger series of reared *L. becki* are available, we will be able to separate the two pupae. The preapical groove of the RO of L.

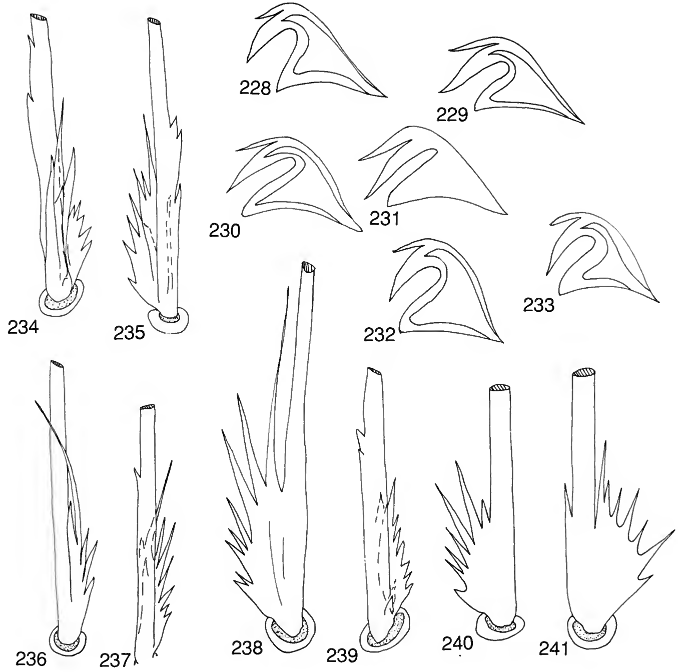


FIGS. 206-227. Larval PPCl and base of SBS. 206-210, *L. maculata;* 206, Cl, Short Creek KA; 207, Cl, MEX; 208. SBS, Short Creek Ka; 209, same, other specimen; 210, SBS, MEX; 211-221, *L. pilosella:* 211, Cl, Savannah River, SC with measurements; 212, Cl, Plum Creek KA; 213, Cl, Illiopolis, IL; 214, Cl, Martin River, NWT; 215, Cl, Gum Creek GA; 216, Cl, Susq. River, PA; 217, Cl, paratype *L. floridana;* 218; SBS, Illiopolis IL; 219, SBS, Potomac River, VA; 220, SBS, paratype *L. floridana*; 221, SBS, Savannah River SC. 222-227, *L. becki:* 222, 223, Cl, Dismal Swamp VA; 224, Cl, Polk Creek, Fl; 225, SBS, Polk Creek Fl; 226, 227, SBS, Dismal Swamp VA.

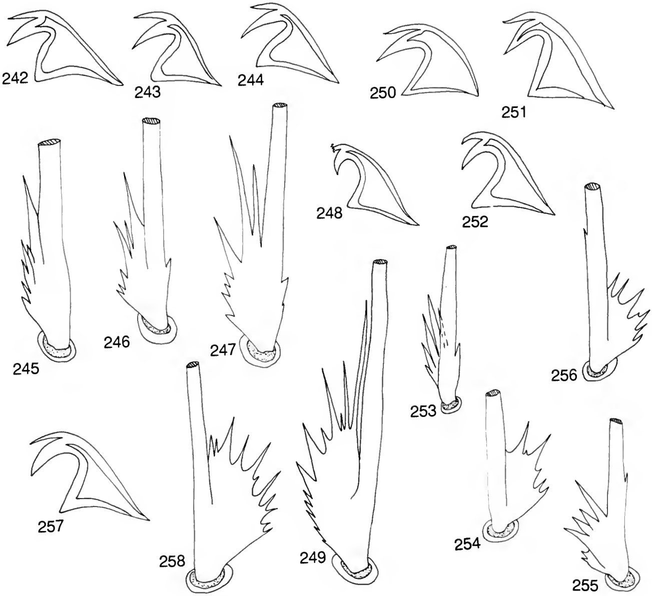
becki appears generally shorter than that of *L. pilosella* but I do not feel there is enough data to establish this character.

PUPA. RO (Figs. 30-32) and thoracic comb (Fig. 5); AeT in Figs. 33, 34; setal pattern of A.IV as in Fig. 14; detail of the ANi, and enclosed AeT in Figs. 33, 34; LS pattern of A.VII, VIII and AL shown in Fig. 82; other characters and measurements given in Table 6.

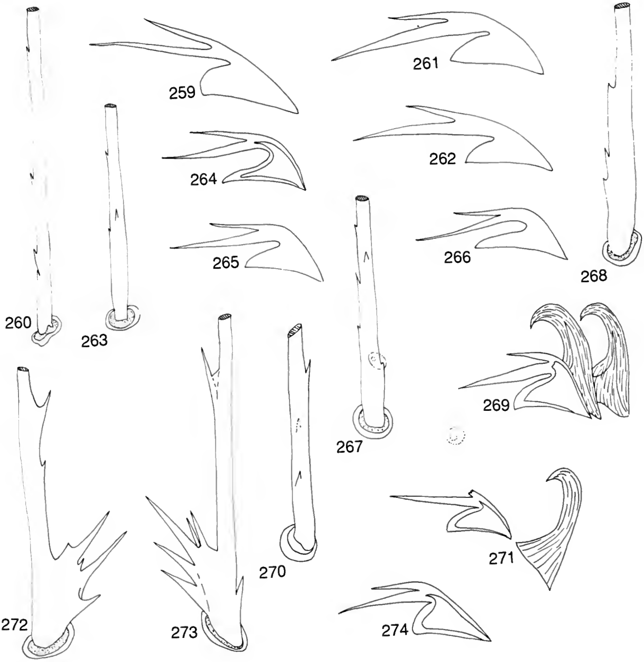
LARVA. Entire head, ventral view, as in Fig 95; head about 432μ L, small LVS group present (Figs. 139-140) but no overall pustules; labrum as in Fig. 119; seta d annulate; antenna similar to Fig. 132; detail CS, A_1 (Fig. 134); MD in Fig. 163; entire maxillary palpus as in Fig. 112; appendages c,d relatively short; Li and PH as in Figs. 184-185; mentum similar to Fig. 123; Pr truncate basally; AP as in Fig. 285; claws of AP



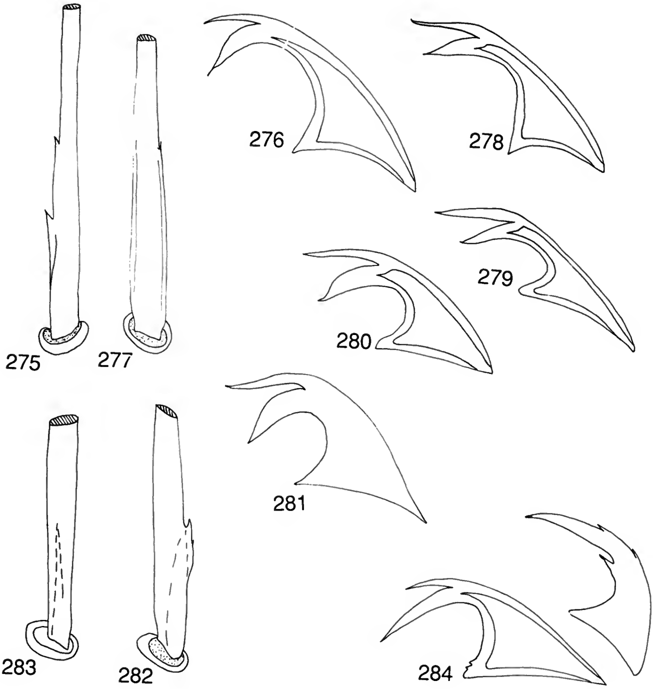
FIGS. 228-241. Larval PPCl and base of SBS. *L. neopilosella:* 228, Cl, ALA; 229, Cl, holotype; 230, Cl, partaype; 231, Shane's Run NJ; 232, Cl, Stewart Co. TN; 233, Cl, Westbrook Pond, AL; 234, SBS, paratype; 235, SBS, Shane's Run NJ. 236, 237, SBS, holotype; 238, SBS, Bay's Mt. Lake, TN; 239, SBS, paratype; 240, SBS, pond, Stewart Co. TN; 241, Westbrook Pond AL.



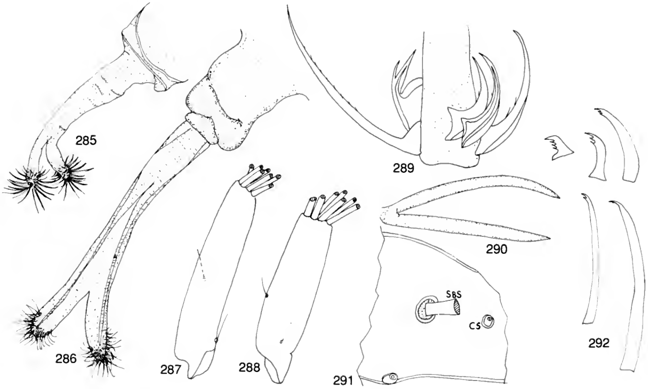
FIGS. 242-258. Larval PPCl and base of SBS. 242-247, *L. neopilosella* var. 4: 242, Cl, Boliek's Pond, FL; 243-344, Cl. Pond #25 KY; 245, SBS, Boliek's Pond FL. 246-247. SBS, Pond #25 KY; 248-249, *L. neopilosella* var. 2: 248, Cl, La Vase R. ONT; 249, SBS, La Vase R. ONT; 250-256, *L. johannseni:* 250. Cl, Alligator River NC; 251, Cl. holotype; 252, Cl,. Cedar Pond TN; 253, SBS, holotype; 254, SBS, Wiccacon Cr. NC; 255, SBS, Cedar Pond TN; 256, SBS, Fisheating Cr. FL. 257-258, *L. neopilosella* var. 3: 257, Cl; 258, SBS.



FIGS. 259-274. Larval PPCl and base of SBS. 259-260, *L. virescens*: 259, Cl, allotype; 260, SBS, paratype; 261-263, *L.* sp. 1 nr. *virescens*: 261, 262, Cl; 263, SBS. 264-267, *L.* sp. 2 nr. *virescens*: 264-266, Cl; 267, SBS; 268-269, *L.* sp. 4: 268, SBS; 269, Cl and dark claws; 270-271, *L.* sp. 2: 270, SBS; 271, Cl and dark claw. 272-274, *L.* sp. 5: 272, 273. SBS; 274, Cl.



FIGS. 275-284. Larval PPCl and base of SBS. 275-276, *L.* sp. 6; 275, SBS; 276, PPCl; 277-280, *L.* sp. 7: 277, SBS. 278-280, Variation in PPCl; 281, 282, *L.* sp. 8: 281, PPCl; 282, SBS; 283- 284, *L.* sp. 9: 283, SBS; 284, PPCl and claw with spinules.



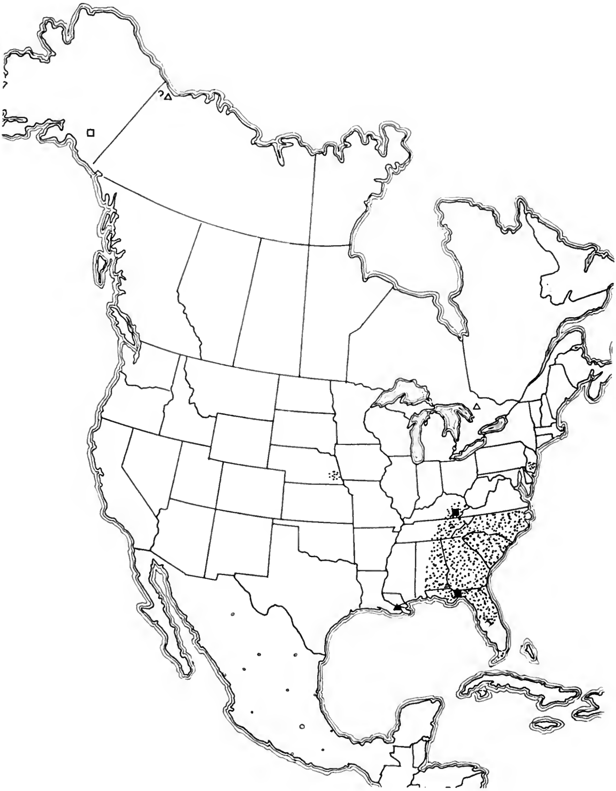
FIGS. 285-292. Larva. 285, AP, *L. maculata;* 286, AP, *L.* sp. 9; 287, Pc, *L. becki;* 288, Pc, *L. pilosella;* 289, apex of PP with claws, *L. becki*; 290, TA, *L.* sp. 1 nr. *virescens;* 291, detail of base of SBS with two possible CS; *L.* sp. 1 nr. *virescens*; 292, claws of AP, *L. pilosella.*

similar to Fig. 292; Pc shown in Fig. 287; SBS generally with two lateral spinules near base (Figs. 225-227); apex of PP and some typical claws in Fig. 289; PPCl variation as in Figs. 222-224; other characters and measurements given in Table 1.

SPECIMENS EXAMINED. **FLORIDA:** 1La, Waddell's Mill Cr., Jackson Co., 7-X-1954, coll. Beck [ANSP]; La, Kissimmee River, Highlands Co., 18-IV-1984, coll. Rutter [FDER]; La, Shell Creek, Charlotte Co., 9-V-1983, coll. Rutter [FDER]; La, Polk Creek, (78) nr. Tallahassee, Leon Co., 7-VI-1972, coll. Roback [ANSP]; mPEx, A, Rayonier forest drainage ditch, Flagler Co., 27-X-1967, coll. Beck [ANSP]; mLa, PEx, A, Little Haw Creek, Flagler Co., 18-VI-1964, coll. Beck [FLSM]. **GEORGIA:** fLa, PEx, A, Pond on I16W, 1 mi E. of Ga 199, 13-III-1986, coll. Caldwell [GDNR]. **NORTH CAROLINA:** La, Little River, Princeton, Johnston Co., IX-1985, coll. Lenat [NC]; La, Basil Creek, Lake Co., V-1986, coll. Lenat [NC]; La, Flat Creek, Durham Co., VIII-1984, coll. Lenat [NC]. **PENNSYLVANIA:** mPEx A, fLa, PEx, A, Lake Lacawac, Wayne Co., 19-IX-1970, coll. Roback [ANSP]. **SOUTH CAROLINA:** 3La, Kingston Swamp at 526-19, Horry Co., 1-VII-1979, coll. White [ANSP]; La, Charles Creek, Anderson Co., 21-IX-1975, coll. Carlson [ANSP]; La, Little Garvin Creek, Anderson Co., 14-VII-1979, coll. White [ANSP]. **TENNESSEE:** La, nr. Lotus Cove, Bays Mt. Lake, 29-IV-1982, coll. Watson [WAT]. **VIRGINIA:** 6La, 2PrP, Portsmouth Ditch, Dismal Swamp, Nansemond Co., 19-IX-1973, coll. Benfield [FLSM]; 3La, Jericho Ditch, same data [FLSM].

L. maculata group

PUPA. RO more triangular or wedge-shaped (Figs. 35-41); preapical groove very shallow (Figs. 42-45); AeT short (Figs. 42-45)



MAP 1. Distribution of *L. neopilosella* group. Stipple = *L. neopilosella*; open square = *L. neopilosella* var. 1; open triangles = *L. neopilosella* var. 2; solid triangle = L. *neopilosella* var. 3; solid squares = *L. neopilosella* var. 4.

LARVA. Head with pustules (Figs. 104, 105); LVS group of head present but faint(Figs, 137, 138); CVS group of head absent no maculation on head (Fig. 104); SBS with basal flag-like spine group (Figs. 208-210); lower spur of bifid claw arched downward toward base plane(Figs. 206, 207); B / C (mean) 0.881

SPECIES. *L. maculata*, *L.* sp. 1

DISTRIBUTION. U.S., Mexico, Trinidad, Venezuela.

This group represented in North America by the single species *L. maculata* is, on the basis of the head, the SBS and the PPCl, somewhat intermediate between the *L. pilosella* and *L. neopilosella* groups. The pupal RO (Figs. 35-41, 75) is distinctive. The pupa, representing *L.* sp.1 from Venezuela is tentatively placed here on the basis of its RO shape. It resembles that of *L. maculata* (Figs. 73, 74) but has a deeper caudal emargination (Fig. 73). Pupae from Trinidad are not separable from those of North American *L. maculata* (Fig. 75).

Labrundinia maculata Roback

Labrundinia maculata Roback 1971: 278.

This species described by the author from California was reared from a rather unusual stream in Kansas by Dr. Ferrington. Superficially, on the basis of the head (Fig. 104) this species resembles *L. pilosella*. However when the SBS (Figs. 208-210) and the PPCl (Figs. 206-207) are examined the relationship of *L. maculata* to the species of the *neopilosella* group becomes apparent. The open arc below the lower PPCl spur and the flag-like base of the SBS are characteristic of the latter group. The pupal RO with its wedge-shape (Fig. 31), lack of a deep preapical groove and short AeT (Figs. 42-45) resembles that of the European *L. longipalpis* (Goetg.) as figured in Fittkau (1962, Fig. 330). On A.IV, seta D_3 is more laterally placed relative to D_1 (Fig. 16) than in *L. pilosella* (Fig. 13). There is a strong possibility that this species is identical with *L. longipalpis* (Goetg.) but more material from Europe and North America will be needed to confirm this.

PUPA. RO wedge sharped (Figs. 35-41); preapical groove indistinct; AeT relatively short and robust (Figs. 42-45); thoracic comb as in Fig. 3; thorax and WP faintly brown; abdomen clear; arrangement of D,L,V setae A.IV in Fig. 16; D_3 laterad of D_1 (Fig. 16); AL and male GS as in Fig. 80, 81; LS, AL with distinct sticky sheaths; detail of apex of AL and its lateral spinules in Fig. 81; other characters and measurements in Table 6.

LARVA Head (Figs. 104, 105) pustulate, with barely evident LVS group, 413-432 μ; details of LVS in Figs. 137, 138; A_1 similar to Fig. 132, detail of apical antennal segments shown in Fig. 136; MD as in Fig. 162; P1 and Pb shown in Fig. 118; detail of lateroventral head setae (SSm, S9, S10) and VP in Fig. 122; Li (Figs. 181-182) with M_t slightly longer than 0; base of Pr similar to Fig. 126; SBS (Figs. 208-210) with flag-like group of 5-7 spines near base; PPCl with inner margin of lower spur almost parallel to inner basal margin (Figs. 206-207); other characters and measurements given in Table 1.

SPECIMENS EXAMINED. UNITED STATES: CALIFORNIA : mA Santee San Diego 27-VII-1962, coll. Perry, [ANSP paratype]; m A Riverside 11-14-IX-1962 [ANSP paratype]. KANSAS : 1PrP, 3m PEx, Short Creek 1.0 mi W. Galena, Cherokee Co., 10-X-1984, coll. Ferrington [KA]; same locality, 3m PA [KA], 1mPA [ANSP]; 1PrP [KA]; 1PrP [ANSP]; 1m La PEx,A (teneral) [KA]; 1La [KA]; 1La [ANSP]; 3m, 1f PEx, Supply Pond at Nelson Reserve, Jefferson Co., coll. Ferrington [KA]. NORTH CAROLINA: f PEx, Belew's Lake, 27-VIII-1962, coll. Wingo [ANSP]; mA, same data (poor specimen) [ANSP]. TEXAS : La, Pedernales River, Blanco Co., 20-V-1981 [WAT}.

MEXICO: COAHUILA : 2La, Ditch S. of Palau on Rt. 94, 19-X-1978, coll. Dunn & Bereza [ANSP].

TRINIDAD: 4fPEx, Hollis Reservior, 15-I-1977, coll. Coffman [COFF].

Labrundinia sp. 1

This species, based on the pupal stage only is placed here on the basis of its shallow preapical RO groove (Fig. 74), the short AeT (Fig. 74) and the basic shape of the RO (Fig. 73) which is close to that of *L. maculata* with a deeper caudal indentation. The RO (Fig. 75) of a probable L. maculata from Trinidad is shown for comparison.

PUPA. RO as in Fig. 73; detail of AN_1 and AeT in Fig. 74; plastron plate small, about 4 µ diameter; thorax, wing pads and abdomen pale; LS placement on A.VII, VIII and AL similar to Fig. 72; other characters and measurements given in Table 6.

SPECIMEN EXAMINED. VENEZUELA: 2m, 4fPEx, Lake Valencia, La Brujita Isl., 27-X-1977 coll.Coffman [COFF].

Labrundinia neopilosella group

PUPA. RO semi-globose (Figs. 46-50, 54); preapical groove indistinct; AeT elongate, appears to follow upper margin of RA (Figs. 51-53).

LARVA. Head without pustules (Figs. 96-98,101-103); LVS group (3-28) present (Figs. 141-148,151); CVS group absent, head without maculation or with transverse band (Figs. 96-98, 101-103); SBS seta with basal flag-like spine group (5-12), one or two may be elongate (Figs. 234-241, 245-247, 249, 253-256); lower spur of bifid claw arched downward toward base plane (Figs. 228-233, 242, 248, 250,2 51, 252); B/C (mean) 0.860-0.971.

SPECIES. *L. neopilosella* , *L. neopilosella* var. 1; *L. neopilosella* var. 2; *L. neopilosella* var. 3; *L. neopilosella* var. 4; *L. johanseni*

DISTRIBUTION. U.S., Canada, Alaska. This appears to be a North American group with its center of distribution in the Southeastern U.S. The single Alaska PEx, *L. neopilosella* var. 1, appears to be *L. neopilosella* but is separated on the basis of its wide geographical separation. The European *L. longipalpis* (Goetg.), on the basis of the larval description (Fittkau & Roback, 1983) appears to fall in this group. The pupal RO, however is close to the *L. maculata* group.

Labrundinia neopilosella

L. neopilosella is a widespread and highly variable species. Its main distribution is southeastern. The first two of the varieties described here are more northern specimens—the pupa from Alaska (var. 1) is larger than any other pupa known to me and is widely separated in distribution from the main *L. neopilosella* distribution. (Map 1). The second (var. 2) is also northern and possesses a distinctive claw of the PP (Fig. 248) and an unusually high number of LVS (Fig. 145). The remaining two varieties are southern and differ in claw shape (Fig. 257) and small number of LVS (Fig. 146) for var. 3 and the caudal head maculation (Fig. 98) and the narrow fork between the lower claw spur and the inner margin (Figs. 242-244) for var. 4. Vars. 2-4 are known only from the larval stage and while they are basically *L. neopilosella* they differed sufficiently, as outlined above, to merit tentative recognition as varietal forms. Only rearing will determine whether they represent new species or are merely extreme variants.

Labrundinia neopilosella Beck and Beck

Labrundinia neopilosella Beck & Beck 1966: 341.
Labrundinia neopilosella: Roback 1971: 278.

PUPA. FA similar to Fig. 6; WP clear; abdomen clear to slightly maculate as in Fig. 13; RO slightly globose; variation shown in Figs. 46-50; AeT relatively elongate, lies along upper margin of RO (Figs. 51-53); preapical groove on RO not evident; thoracic comb similar to Fig. 4; abdominal setae appear similar to *L. pilosella* (Fig. 13); AL as in Fig. 83 (dorsal) and Fig. 87 (lateral); detail of tip of AL as in Fig 84; other characters and measurements given in Table 7.

LARVA. Head shape and LVS as in Figs. 96,97; 394-444µ L; variation in LVS group as in Figs. 141-144; labrum similar to Fig. 119; MD as in Fig. 164; P_1 and P_b shown in Fig. 116; Li and Pl as in Figs. 189-191; M_t always longest; variation in Li teeth in Figs. 189-191; base of Pr similar to Fig. 123; SBS with basal spines forming flag-like group with one or two spines very elongate; holotype as in Figs. 236, 237; other variants in

Table 2. Comparison of range of measurements (µ) and ratios for larvave of the *L. neopilosella* group. Numbers in [ ] = n for means. A = absent, P = present.

	L. neopilosella [8]		var. 2	var. 3	var.4 [3]		L. johannseni [5]	
	r	mean			r	mean	r	mean
H-pustules	-A	-	-A	A	-A	-	-A	-
H-Mac.C	-A	-	A	-A	-0.3	-	-A	-
H-Mac. V	-A	-	-A	-A	-A	-	-P	-
H-LVS	6-15	10.7[7]	28	3	7-10	8.3	7-13	8.9[4]
H-CVS	-A	-	-A	-A	-A	-	-A	-
A_1-L	178-199	185	189	185	181-189	185	178-192	183.4
A_2-L	66-73	69.4[7]	80	68	67-78	71.7	67-78	71.2
AR	2.29-270	2.455	2.15	2.37	2.15-2.76	2.5	2.20-2.45	2.33
MD-L	61-73	69	73	72	68-73	70.3	66-76	69.8
ApT-L/W	2.5	-	2	2.1	2.0-2.4	2.18	2.22-267	2.445[2]
ApT/MD	0.20-0.20	200[2]	0.19	0.21	-0.21	-	0.20-0.26	0.230[2]
A_1/MD	2.57-2.92	2.686	2.59	2.57-	2.59	-	2.38-2.76	2.632
P_1L	22-28	25.3[7]	23	22	22-23	22.7	22-25	23.4
P_1L/W	2.50-3.80	3.386[7]	3.2	3	3.0-3.2	3.13	2.83-3.20	3.024
CS,P_1	0.70-0.82	0.778[5]	-	-	-	0.18	0.80-0.80	0.800[2]
A_1/P_1	6.36-8.09	7.410[7]	8.22	8.41	7.75-8.59	8.09	7.24-8.35	7.862
Li-L(O)	45-50	47.2[6]	48	50	47-51	48.3	43.51	47.6
It/O	0.97-1.00	0.986[6]	1	0.99	0.92-0.99	0.98	0.84-0.98	0.968
Mt/O	1.10-1.13	1.120[6]	1.12	1.07	1.05-1.11	1.07	1.06-1.13	1.092
Pl-L	23-28	25.8[4]	-	28	25-29	27.0[2]	25-28	26.8[4]
no. teeth PH	7-8	7.7[3]	-	8	-9	-	-8	-
Pc-L	111-167	136.5[6]	141	118	108-144	127.3	122-155	135.4
PC-L/W	4.71-5.63	5.222[5]	4.75	4.27	4.67-4.88	4.243	4.50-5.25	4.878
PPCl-A	42-51	47.6	-	49	38-46	42.7	41-46	43.8
PPCl-B	58-67	61.9	-	67	51-65	56.7	50-65	58.0[5]
PPCl-C	57-67	63.6	-	72	61-70	64.7	58-72	64.6
B/C	0.95-1.02	0.971	-	0.86	0.84-0.92	0.873	0.86-0.92	0.898
access dk. cl.	-A	-	-A	-A	-	-A	-	-A

Figs. 234, 235, 238, 241; bifid claw of PP with lower claw almost parallel to inner margin; variation in Figs. 228-233; other characters and measurements given in Table 2.

SPECIMENS EXAMINED. **ALABAMA** : 2La (IV), 1La (III) Westbrook Pond, Orville, Dallas Co., 25-VII-1986, coll Griffiths [ANSP]; 1La, same locality 4-IX-1986. **FLORIDA** : mLa, A, Rayonier Ditch, Flagler Co, 3-VI-1964, coll Beck [USNM Holotype 69125]; fLa, PEx, A, same data [ANSP, paratype]; mLa, PEx, A, same locality, 27-II-1965, [ANSP]; fLa, PEx, A, Bolieks Pond, Leon Co., 11-V-1965, coll Beck [FLSM, paratype]; mLa, PEx, A, Santa Fe River, Alachua Co., 13-X-1967, coll. Beck [WINN]; 2PrP, Kissimmee R. Highlands Co., 7-VIII-1984, coll. Rutter [FDER]. **GEORGIA** : 4 La, Lake Whitney, Cumberland Isl., 17-V-1977, coll. Smock [ANSP]; La, same locality, VII-1977 coll. Lenat [NC]; -fPEx, A, J. Kurze's Farm, Sandfort, Russell Co., 25-V-1981, coll. Heyn [ANSP]; m,fLa, PEx, A, Millrock Branch, Haralson Mill Rd., Rockdale Co., 20-IV-1982, coll. Caldwell [GDNR]. **KENTUCKY** : 3La, Pond #5, Old Ferry Rd., N. of Dickerson Cen., Lyon Co., coll. Watson [WAT]; La, 2PrP, Pond #15, Wildlife Restoration Center, Lyon Co., 11- VIII-1986, coll. Watson [WAT]; La, Pond #17, Trigg Co., 12-VII-1986, coll. Watson [WAT]. **NEBRASKA** : 2La, Long Creek Loop, Missouri Riv., 19-VIII-1975 [ANSP]; La, same locality 20-X-1975 [ANSP] . **NEW JERSEY** : La, Shane's Run, Friendship (51), 11-VIII-1953, coll. Roback [ANSP]. **NORTH CAROLINA**: f PEx, Mill Creek Pond, 22-X-1976, coll. Coffman [COFF]; 2La, Belew's Lake, Stokes Co., 16-IX-1985, coll. Wilda [ANSP]; 2La, same locality, VIII-1973, coll. Lenat [NC]; 9La, Belew's Lake, Forsyth Co., 16-IX-1985, coll. Wilda [ANSP]; La, same locality, 24-IX-1985, [ANSP]; La, White Oak River, Onslow Co., VII-1984, coll. Lenat [NC]; PrP, Salem Lake, Forsyth Co., IX-1982, coll. Lenat [NC] La, Belew's Creek, Stokes Co., 7-VIII-1972, coll. Lenat [ANSP]. **SOUTH CAROLINA**: 2La, Fish Pond at SE end of Simpson Sta., Anderson Co., 25-III-1977, coll. White & Carlson [ANSP]; fP, Jocassee Reservoir, Salem, Oconee Co., 16-VIII-1974, coll. Hudson [ANSP]. **TENNESSEE**: La, Bay's Mt. Lake, Sullivan Co., 13-IX-1979, coll. Watson [ANSP]; La, same locality 25-VII-1981 [WAT]; La (III) same locality 14-IV-1986 [WAT]; m, fPEx, same locality 30-V-1985 [WAT]; f PEx, same locality, 3-IX-1985 [WAT]; m PEx, Ecology Pond, Bay's Mt. Lake, 29-IV-1985, coll. Watson [WAT]; 4f PEx, same locality, 30-V-1985 [WAT]; 3La, Pond at intersection Rts. 230, 399, Stewart Co., 18-VII- 1986, coll. Watson [WAT]; La, Pond #29 (Cedar Pond) Stewart Co., 19-VII-1986 coll. Watson [WAT].

Labrundinia neopilosella var. 1

This var. is separated on the basis of its larger size and disjunct distribution (Map. 1). Figures 54 (RO) 85 (AL) and 86 (apex AL) and the measurements in Table 7 will serve to delineate this var.

ALASKA : fPEx, Fish Creek, nr. Nenana (S.E. of Fairbanks), 19-VII-1978, coll. Wartinbee [COFF].

Labrundinia neopilosella var. 2

This var. from North Bay, Ontario is separated on the basis of the high no. of spines in the LVS group (Fig. 145) the sharply hooked lower spur of the furcate claw of the PP (Fig. 248) and the long A_2 (Table 2, Fig. 132). The upper spur of the PPCl is broken. The Mackenzie Delta specimen is poor and its placement here is tentative.

LARVA. LVS group of head as in Fig. 145; antenna shown in Fig. 132; apical teeth of Li in Fig. 197; base of SBS, strongly flag-like (Fig. 249); broken PPCl (Fig. 248); other characters and measurements in Table 2.

SPECIMENS EXAMINED. **CANADA - ONTARIO** : La, La Vase River at Rt. 11, North Bay, 24-IX-1971, coll. Roback [ANSP]. **NORTHWEST TERRITORIES**: La, Mackenzie River Delta, 68° 02'N, 134°49'W, 27-VII-1972 [CNC].

Labrundinia neopilosella var. 3

This var. represented by a single speciemen from Louisiana is separated on the basis of the very small head LVS spur group (Fig. 146) and the broadly rounded and open groove of the PPCl (Fig. 257) which resembles that of *L. johannseni* (Figs. 250-252).

LARVA. Li as in Fig. 194; LVS spur group of head reduced (Fig. 146); SBS seta with basal spines not elongate (Fig. 258); PPCl as in Fig. 257; other characters and measurements in Table 2.

SPECIMENS EXAMINED. **LOUISIANA**: La, Reserve Canal nr. Reserve, 21-X-1968, coll. Roback [ANSP].

Labrundinia neopilosella var. 4

In this var. the lower spur of the bifid claw is more divergent from the base (Figs. 242-244) and the head appears pale brown in the posterior third (Fig. 98). The head LVS group does not differ from that of the nominate species. There is some question in my mind regarding the Kentucky specimens but they seem to belong here.

LARVA. Head as in Fig. 98; LVS group as in Fig. 147 (FL) and Fig. 148 (KY): Li and Pl as in Figs. 192-193; variation in basal spines group of SBS shown in Figs. 245-247; PPCl variation in Figs. 242-244; other characters and measurements given in Table 2.

SPECIMENS EXAMINED. **FLORIDA**: La, Boliek's Pond, Leon Co., 11-V-1965, coll. Beck [FLSM]. **KENTUCKY**: 4La, Pond #25, Devil's Elbow Lake access, Trigg Co., 13-VII- 1986, coll. Watson 2La [WAT]; 3La, Pond #28, TVA-LVL, Trigg Co., 15-VII-1986, coll. Watson [WAT].

Labrundinia johannseni Beck & Beck

Labrundinia johannseni Beck & Beck 1966: 342.
Labrundinia johannseni:Roback 1971: 279.

This is a moderately abundant southeastern species. The larva is easily recognizeable on the basis of the mesal head band (Figs. 101-103) which almost encircles the head and the form of the PPCl (Figs. 250-252) with its wide lower groove. Some of the larval vars. of *L. neopilosella* closely resemble *L. johannseni* but lack the head maculation. The pupa, except for the slightly more globose RO is not easily separable from that of *L. neopilosella*. There are very few rearings available and consequently few clearly assignable pupae.

PUPA. RO as in Figs. 55-56; globose in shape, easily distorted in mounting; detail of the ANi and the AeT in Figs. 57, 58; WP and abdominal tergites pale brown; placement of LS.VII, VIII and AL in Fig. 88; other characters and measurements given in Table 7.

LARVA. Head marked as in Figs. 101-103; dorsal portion of band fainter; head about 480m L; IC about 0.50; maximum depth/length also 0.50; LVS group as in Figs. 103, 151; labrum similar to Fig. 119; MD as in Fig. 166; Pl similar to that of *L. neopilosella* (Fig. 116); Li, Pl and PH of holotype in Fig. 196; Li with M_t longest as in Figs. 195-196; base of Pr similar to Fig 126; variation in flag-like basal spines of SBS in Figs 253-256; PPCl variation shown in Figs. 250-252; other characters and measurements given in Table 2.

SPECIMENS EXAMINED. **FLORIDA**: La, Fisheating Creek, Glades Co., 20-V-1975, coll. Rutter [FDER]; La, Arbuckle Creek, Highlands Co., 27-VII-1983, coll. Rutter [FDER]; 2PrP, same locality, 3-II-1987, coll. Rutter [ANSP]; mLa, PEx, A, Rayonier Ditch, Flagler Co., 30-I-1965, coll. Beck [USNM holotype 69126]; 2La, fPEx, A, same data, [ANSP]; La, same locality, 27-X-1967, coll. Beck [ANSP]; La, Shingle Creek, Orange Co., 14-I-1958, coll. Beck [ANSP]; La, Blackwater River at Wright Basin, Rosa Co., 18-VIII-1976, coll. Bass [ANSP]; La, Escambia River, Escambia Co., 6-VIII-1958, coll. Beck [ANSP]; PrP, Swift Creek, Hamilton Co., 8-XII-1966, coll. Beck [ANSP]. **GEORGIA**: mA, Little Attapulgus Creek, Decatur Co., 7-XI-1984, coll. Caldwell [GDNR]; La, Little River below Hway. 37, Cook, Colquitt Co. line, 6-IX- 1972, coll. Caldwell & Kennedy [GDNR]. **NORTH CAROLINA**: 2La, Nense River, Carven Co., VII-1985, coll. Lenat [NC]; -La, Lockwoods Folly River, Brunswick Co., VII-1984, coll. Lenat [NC]; La, Alligator River, Tyrell Co., VII-1984, coll. Lenat [NC]; 2La, Wiccacon River, Hartford Co., VII-1985, coll. Lenat [NC]; La, Chowan River, Hartford Co., VIII-1981, coll. Lenat [NC]; 2La, Deep River, Randolph Co., VIII-1972, coll. Lenat [NC]. **TENNESSEE**: 5La, Pond #29 (Cedar Pond), Stewart Co., 19-VII-1986, coll. Watson [WAT].

L. virescens group

PUPA. RO large with S-shaped RA (Figs. 59, 60, 62-64, 68); preapical groove long (Figs. 61, 65, 70); spinules on AL large (Fig. 76, 90, 92); hump present on A.III-VII (Fig. 15).

LARVA. Head without pustules; LVS group (2-7) present (Fig. 149); CVS group absent; no maculation on head; SBS with 1-4 small lateral spines (Figs. 260, 263, 267, 270) lower spur of PPCl parallel to basal plane, relatively long (Figs. 259, 261, 262, 264-266, 271); B/C (mean) 1.243-1.425

SPECIES. *L. virescens; L.* sp. 1 nr. *virescens*; *L.* sp. 2 nr. *virescens*; *L.* sp. 3 nr. *virescens*; *L.* sp. 2; *L.* sp. 3

DISTRIBUTION. S.E. U.S., Cuba, Colombia, Venezuela.

This group distinguished by the form of the bifid claw of the larval PP and the shape (as far as known) of the RA (Figs. 59, 60, 62-64). appears to be primarily Neotropical. In the U.S. there are only one or two species, very sparsely represented in the S.E., US. The possibility exists that *L.* sp. 4 (group A) may ultimately belong here. *L.* sp. 3 nr. *virescens* (pupa) is placed here on the basis of its resemblance to that of *L. virescens*.

Labrundinia virescens Beck & Beck

Labrundinia virescens Beck & Beck1966: 341.
Labrundinia virescens: Roback 1971: 279.
Labrundinia pilosella: Fittkau & Murray 1986: 85, Figs A,D-I

This is one of the largest of the *Labrundinia* species and appears to be one of the U.S. representatives of a primarily Neotropical species group. *L.* sp. 3 nr. *virescens* (pupa only) also appears to be related to *L. virescens* on the basis of its RO (Fig. 59, 60). *L. virescens* is, to-date, scarce in collections and the only pupae available belong to the type series.

PUPA. RO large with S-shaped RA; both grooves deep and narrow (Figs 59, 60); AeT elongate extends from upper surface of preapical groove into ANi (Fig. 61); thoracic comb, arcuate with second spur smaller similar to that in Fig. 2; thorax pale brown; WP pale brown; A.IV and setae similar to in Fig. 15; hump present on A.III-VII, not as pronounced as in Fig. 15; LS.VII, VIII and AL as in Fig. 89; lateral spines of AL very large; detail of apex AL in Fig. 90; other characters and measurements given in Table 8.

LARVA. Head pale, no pustules; about 500μ L: LVS group present (Fig. 149); labrum similar to Fig. 119; detail of annulate d-seta in Fig. 120; base of Pr similar to Fig 125; MD as in Fig. 165; basal inner tooth spinose; P_1 elongate (Fig. 115); Li and Pl large, paratype in Fig. 198, tip of allotype Li (Fig. 199); SBS (Fig. 260) with only a few small spinules along shaft; PPCl with elongate lower spur, parallel to base (Fig. 259); other characters and measurements given in Table 3.

SPECIMENS EXAMINED. **GEORGIA** : La, Lake Whitney, Cumberland Isl., 21-IX-1977, coll. Lenat [NC]. **FLORIDA** : La, Horse Creek, Desoto Co., 5-V-1976, coll. Ruther [FDER]: mLa, PEx, A Boliek's Pond, Leon Co., 30-VI-1964, coll. Beck [USNM Holotype 69 124]; f La, PEx, A, 5-V-1964, coll. Beck [USNM Holotype 69124]; fLa, PEx, A, 30-VI-1964, coll Beck [ANSP, paratype]; La 22-VII-1965 [ANSP]; La, Sphagnum ditch, St. John's Co., 17-XI-1967, coll. Beck [ANSP].

The following two species *L.* sp.1 nr. *virescens* and *L.* sp. 2 nr. *virescens* are both from the same pool nr. Hacienda El Viento in Colombia. They differ in the smaller size of *L.* sp. 2 nr. *virescens*. The A_2 MD and Li of the latter species are clearly smaller but A_1 and P_1 are in the same range as *L.* sp.1 nr. *virescens* (see Table 3). Both are known only from the larval stage and the separation is naturally tentative.

Labrundinia sp.1 nr. virescens Beck & Beck

LARVA. Head clear; LVS group as in Fig. 152; apex of MD in Fig. 169; lower inner tooth spinose; base of Pr similar to Fig. 125; Li and Pl shown in Fig. 202; base of SBS with few small spinules in Fig. 263; detail of base of SBS with possible CS in Fig. 291; PPCl with long lower spur (Figs 261, 262), TA as in Fig. 290; other characters and measurements given in Table 3.

SPECIMENS EXAMINED. COLOMBIA: 4 La, Pond at Hacienda El Viento, 32 km ENE of Puerto Lopez, Dept. del Meta, 10-XII-1969, coll. Roback [ANSP].

Labrundinia sp. 2 nr. **virescens** Beck & Beck

LARVA. Head clear; LVS group similar to Fig. 152; Li and Pl shown in Fig. 203; MD as in Fig. 170; base Pr truncate (Fig. 125); SBS with few spinules near base and two possible CS in Fig. 267; PPCl variation in Figs 264-266; lower groove more rounded than in *L.* sp. 1 nr. *virescens* (Fig. 261, 262); other characters and measurements given in Table 3.

SPECIMENS EXAMINED. COLOMBIA: 3 La, Pond at Hacienda El Viento, 32 km ENE of Puerto Lopez, Dept del Meta, 10-XII-1969 coll. Roback [ANSP].

Labrundinia sp. 3 nr. **virescens** Beck & Beck

This pupa, very close to that of *L. virescens* (see Figs. 91-93 and Fig. 62-64) is restricted to the southeastern U.S. As noted under *Labrundinia* sp. 4 it may belong with that larva but has never been reared. It differs from that of *L. virescens* in the more open S of the RA (Figs 62-64) and the shorter and fewer lateral spines on the AL (Figs. 92-94). *Labrundinia* sp. from Florida

Table 3. Comparison of range of measurements (μ) and ratios for larvae of the *L. virescens* group. Numbers in [ ] = n for means. A = absent, P = present.

	L. virescens [4]		L. sp. 1 nr. virescens [4]		L. sp. 2 nr. virescens [3]		L. sp. 2.
	r	mean	r	mean	r	mean	
H-pustules	-A	-	-A	-	-A	-	A
H-Mac.C	-A	-	-A	-	-A	-	A
H-Mac. V	-A	-	-A	-	-A	-	A
H-LVS	3-6	4.3	2-7	4.3[3]	2-3	2.5[2]	3-4
H-CVS	-A	-	-A	-	-A	-	A
A_1-L	252-356	277.5[2]	237-244	240.8	211-241	231.0	241
A_2-L	90-118	1.6.0[2]	92-93	92.5[2]	60-70	66.0[2]	-
AR	2.29-2.35	2.310[3]	2.25-2.44	2.345[2]	2.60-2.98	2.790[2]	-
MD-L	111-124	118.3	102-108	104.8[6]	76-88	82.2[2]-	80
ApT-L/W	2.17-2.53	2.348	2.94-3.13	3.035[2]	-2.13	-	-
ApT/MD	0.30-0.34	0.318	0.34-0.36	0.350[2]	-0.27	-	-
A_1/MD	2.17-2.47	2.370[3]	2.23-2.35	2.3	2.74-2.78	2.760[2]	3.01
P_1L	35-44	70	34-37	35.3[3]	31-35	33.3	28
P_1L/W	4.00-5.00	4.493	3.83-4.17	4.000[3]	4.00-4.60	4.267	3.8
CS.P_1	-0.86	-	0.84-0.88	0.867[3]	-0.86	-	-
A_1/ P_1	7.29-7.51	7.403[3]	6.51-7.09	6.790[3]	6.81-7.08	6.846	8.61
Li-L(O)	68-83	77	70-73	71.3	56-57	56.5[2]	58
It/O	0.86-0.91	0.888	0.87-0.90	0.883	0.83-0.90	0.865[2]	0.9
Mt/O	0.96-1.01	0.993	0.99-1.00	0.995	0.99-1.00	0.995[2]	1.00
Pl-L	-37	-	29-34	31.7[3]	28-30	28.7[2]	29
no. teeth PH	-7	-	6-7	6.2[3]	6-6	6.0[2]	-
Pc-L	207-229	218.3	192-203	195.8	140-170	160.0	218
PC-L/W	6.67-8.86	7.565	6.88-7.57	7.15	6.33-7.67	6.857	8.43
PPCl-A	45-52	48.5[2]	47-51	49.3[3]	44-50	47.0	38
PPCl-B	93-110	101.5[2]	95-108	102.7[3]	76-80	77.3	76
PPCl-C	58-88	73.0[2]	67-80	75.3[3]	57-67	62.3	?
B/C	1.25-1.60	1.425[2]	1.33-1.42	1.367[3]	1.19-1.33	1.243	-
access dk. cl.	A	-	A	-	-1		1

shown in Fig. 5.19C in Fittkau and Murray (1986) appears to belong to this species.

PUPA. RO as in Figs. 62-64; detail of ANi and AeT in Fig. 65; thoracic comb arcuate (Fig.2); thorax pale brown; wing pads clear; abdomen clear to pale brown; A.IV similar to Fig 15; mild hump similar to Fig. 15 on A.III-VII; LS, VII, VIII and AL of male in Fig. 91; detail of apex of AL with spinules in Fig. 92; female AL and GS in Fig. 93; other characters and measurements given in Table 8.

SPECIMENS EXAMINED. NORTH CAROLINA: Belew's Lake mPEx 16-IX-1985, Stokes Co., coll. Wilda [DP]; mf PEx 24-X-1985, Forsyth Co., coll. Wilda [ANSP]; f PEx 5-X-1976, coll. Wingo [ANSP]; fmA 5-X-1976, coll. Wingo [ANSP]; mA, Belew's Lake (poor specimen) 5-X-1976, coll. Wingo [ANSP].

Labrundinia sp. 2

This species, represented by a single, poorly mounted larva from Cuba, is tentatively placed in the *L. virescens* group on the basis of the immaculate head with only a small LVS group, the truncate base of the Pr (Fig.127) and the long lower spur of the PPCl (Fig. 271). Unfortunately the upper spur is broken. There is a single dark claw (Fig. 271) associated with the PPCl. *L.* sp. 4, possibly associated with *L.* sp. 3 nr *virescens* has two such dark claws (Fig. 269).

LARVA. Head clear; LVS group of 3-4 spurs (Fig. 153); base of Pr as in Fig. 127; Li and Pl shown in Fig. 205; base of SBS with 3 lateral basal spinules (Fig. 270); broken PPCl and dark claw in Fig. 271; other characters and measurements given in Table 3.

SPECIMENS EXAMINED. CUBA: La, El Dique, La Habana, 23 /O1N, 32/14W, 4-XII-1968, coll.. Hruska [ANSP].

Labrundinia sp. 3

This species is on the basis of the large spines on the AL (Fig. 76), related to *L. virescens* and *L.* sp. 3 nr. *virescens.* Unfortunately the single female pupa available is in very poor condition and lacks the RO. The LS filament placement on A. VII, VIII could not be measured. Fig. 76 and the measurements in Table 8 will, for the present, serve to define this taxon. It is not sufficiently distinctive to place in the key to pupae.

. SPECIMEN EXAMINED. VENEZUELA: fP, EL Limon, 27-VI-1974, coll. Coffman [COFF].

Group A

LARVA. Head without pustules (Fig. 99-100); LVS group consists of a single large spine (Figs. 150) CVS group (13-14) present (Fig. 99-100); no maculation on head; SBS with 3 small lateral spinules near base (Fig. 268); lower spur of PPCl claw parallel to basal plane (Fig. 269); two dark heavy claws associated with bifid claw (Fig. 269); B/C (mean) 1.173

SPECIES. *L.* sp. 4.

DISTRIBUTION. S.E., U.S.

This larva, when associated probably will fall in the *L. virescens* group. It is tentatively separated from that group on the basis of the single LVS spur (Fig. 150), the presence of a CVS group (Figs. 99-100), and the two dark claws associated with the PPCl (Fig. 269).

Labrundinia sp. 4

This unusual species, based on the larva only, is characterized by the large single LVS spur (a small second is occasionally found) and the two dark claws (Fig. 269) associated with the PPCl. In a manuscript key internally circulated by Mr. R. P. Rutter (Florida DER) it is called *L.* sp.1 - Cantrell. In Belew's Lake NC it is found along with PEx of *L.* sp. 3 nr. *virescens* but the two have not been clearly associated by rearing or a mature PrP.

Head as in Figs 99, 100; 463-481 µ L; LVS group (Fig. 150) single; CVS group as in Figs. 99, 100; base of Pr truncate into internal ridge (Fig. 124); MD as in Figs. 167, 168; P_t and P_b shown in Fig. 117; Li (Fig. 200) of *virescens* type, with $M_t = 0$; PH as in Fig. 201; SBS with only 2-3 small lateral spinules (Fig. 268); PPCl of *virescens* type

(Fig. 269). Two dark claws associated with PPCl; other characters and measurements given in Table 4.

SPECIMENS EXAMINED. **ALABAMA :** 3La, Westbrook Pond, Orville, Dallas Co., 24-V-1986, coll. Griffiths [ANSP]; 2La, same locality, 10-VI-1986; 1La, same locality 14-VI-1986. **FLORIDA :** La, Canal Parkway, C-13, Broward Co., 7-VII-1961, coll. Beck [ANSP]; La Withlacoochie River, Madison Co., 20-VII-1955, coll. Beck [ANSP]; La, Bear Branch P-58, Polk, Co., 27-VII-1955, coll. Beck [ANSP]; La, Lehigh Canal, Lee Co., coll. Rutter [FDER]. **NORTH CAROLINA :** La, Salem Lake, Forsyth Co., IX-1983, coll. Lenat [NC] -5La, Belew's Lake, Stokes Co. 16-IX-1985, coll. Wilda, [ANSP]; La(II), La (III), Belew's Lake, Forsyth Co. 16-IX-1985, coll. Wilda [ANSP]. **SOUTH CAROLINA:** La, Cooper River, nr. Richmond Plantation, Berkley Co., 30-VIII-1973, coll. Richardson [ANSP].

Group B

LARVA. Head without pustules; Pl multi-branched (Fig. 204); LVS group appears present but indistinct CVS group absent no maculation or head; SBS with irregular arrangement (5+2) of spines (Figs. 272, 273); lower spur of bifid claw elongate parallel to basal plane (Fig. 274); B/C 1.21.

SPECIES. *L.* sp. 5.

DISTRIBUTION. Colombia.

This group represented by a single larva is, on the basis of the PPCl, close to the *L. virescens*

Table 4. Comparison of range of measurements (μ) and ratios for larvae of the *Labrundinea* groups A and B. Numbers in [ ] = n for means. A = absent, P = present.

	L. sp. 4 [6]		L. sp. 5
	r	mean	
H-pustules	-A	-	A
H-Mac.C	-A	-	A
H-Mac. V	-A		A
H-LVS	1-1	1[3]	A
H-CVS	13-14	13.5[2]	?
A_1-L	207-299	212.5	263
A_2-L	76-85	79.8[4]	89
AR	2.23-2.40	2.313[4]	2.63
MD-L	80-92	85.7	67
ApT-L/W	-2.57	-	2.5
ApT/MD	0.27-0.30	0.285[2]	0.22
A_1/MD	2.35-2.54	2.482	3.92
P_1L	32-39	34.8[5]	22
P_1L/W	3.60-4.80	4.350[5]	3.00
CS,P_1	0.83-0.90	0.865[2]	0.73
A_1/P_1'	6.03-6.41	6.174[5]	11.90
Li-L(O)	61-70	64.4[5]	50
It/O	0.89-0.99	0.930[5]	0.96
Mt/O	1.00-1.02	1.004[5]	1.00
Pl-L	29-31	30.1[3]	28
no. teeth PH	7-8	7.5[2]	7
Pc-L	141-170	153.8[5]	167
PC-L/W	5.11-8.33	6.076[5]	5.29
PPCl-A	42-47	43.2	50
PPCl-B	70-79	73.7	91
PPCl-C	55-69	63.0	75
B/C	1.09-1.27	1.173	1.21
access dk. cl.	2-2	2.0[5]	A

group but differs in the structure of the SBS (Figs. 272, 273) and the Pl (Fig. 204).

Labrundinia sp. 5

The unusual SBS (Figs. 272, 273) and the Pl with its three small outer teeth (Fig. 204) will distinguish this species. The larva is in poor condition. The LVS group is indistinct and no head measurements could be taken.

LARVA. Head with LVS group indistinct. No pustules or maculation; Li and Pl as in Fig. 204; Pr fades out apically and basally ends between arms of internal plate below submentum (Fig. 129); SBS with two spinule groups (Figs. 272, 273); PPCl (Fig. 274) similar to *L. virescens* group; other characters and measurements given in Table 4.

SPECIMENS EXAMINED. COLOMBIA: La, Pond #3 on Hacienda Mozambique, 16km. SW of Puerto Lopez, Dept. del Meta, 1-III-1971, coll. Roback [ANSP].

Group C

LARVA. Head with pustules (Figs. 107-111); LVS group present on head (Figs. 154, 156, 158); CVS group present on head (Figs. 155, 157, 159, 160); maculation of head present, W shaped (Figs. 106, 111) or quadrate (Figs. 107, 109, 110); SBS seta of PP with 1-2 small spinules near base (Figs. 275, 279, 282, 283); lower spur of bifid claw of PP arched away from basal plane (Figs. 276, 278-281, 284); B/C (mean) 0.750-1.08

SPECIES. *L.* sp. 6; *L.* sp. 7; *L.* sp. 8; *L.* sp. 9.

DISTRIBUTION. S.E. U.S., Cuba, Colombia.

Like the *L. virescens* group, this appears to be primarily a Neotropical group which extends northward into the US (*L.* sp. 6). Unfortunately no pupae were associated with any of the larvae. The only North America representative, *L.* sp. 6 is listed as *L.* sp. 1 in Lenat (1984).

Labrundinia sp. 6

This is the species keyed as *L.* sp. 1 by Lenat (1984). It appears to be the northern representative of a primarily Neotropical group. No pupa has been associated with it to-date.

LARVA. Head maculation and pustules as in Fig 109; detail of LVS and CVS groups of head in Figs. 154, 155; apex of MD (Fig. 172); P1 shown in Fig. 113; Li, Pl and PH given in Fig. 186; base of Pr between arms of internal head ridge (Fig. 131); SBS with 1-2 basal spinules (Fig. 275); PPCl widely arched from base (Fig. 276); other characters and mesurements given in Table 5.

SPECIMENS EXAMINED. **FLORIDA** : Prp, Jack's Creek, Highlands Co., 18-III-1981, coll. Rutter [FDER]. **GEORGIA** : 2PrP Swift Creek at GA 152, Toombs Co., 24-IX-1979, coll. Caldwell & Hennessy, 1-[ANSP], 1-[GDNR]; 3La, Lake Whitney, Cumberland Isl., IX-1977, coll. Lenat [NC]; 1La, same locality, VII-1977 [NC]. **KENTUCKY** : La, Pond #17, Trigg Co., 12-VII-1986, coll. Watson [WAT]. **NORTH CAROLINA** : La, Mackey's Creek, Washington Co., VI-1983, coll. Lenat [NC]. **TENNESSEE**: La, Pond #29 (Cedar Pond), Stewart Co., 19-VII-1986, coll. Watson [WAT].

Labrundinia sp. 7

This species resembling *L.* sp. 8 was found only in a small, dry forest pool. It and *L.* sp. 8 are possily variants of a single widespread species. The only pupa found was, unfortunately, a poor specimen lacking respiratory organs. Superficially it resembled the pupa described as *L.* sp. 10

LARVA. Head about 480 µ L; general maculation and pustules as in Fig. 108; detail of LVS and CVS groups in Figs. 156, 157; the lateroventral head setae and VP are arranged as in Fig. 121; details of the base of A_1 and apex of antenna in Figs. 133, 135; MD shaped as in Fig. 173; Li shown in Fig. 187; entire mentum with base of Pr between arms of internal ridge (Fig. 128); SBS almost completely simple, only one lateral spinule (Fig. 277): variation of PPCl as in Figs. 278-280; other characters and measurements given in Table 5.

SPECIMENS EXAMINED. COLOMBIA: 5La, mP, Pond near a dry forest on property next to Hacienda Mozambique, 16km SW of Puerto Lopez, Dept. del Meta, 11-XII-1969, coll. Roback [ANSP].

Labrundinia sp. 8

This species found only at two or three localities in Cuba is possibly a variant of *L.* sp. 7. It is separated on the basis of some PPCl differences from *L.* sp. 7 and on its distribution.

LARVA. Head 451-480 µ L; variation in maculation and spurs in Figs. 110, 111; detail of LVS and CVS in Figs. 158,159; variation in tip of MD as in Figs. 175, 176; P_1 given in Fig. 114; L_1 and PH as in Fig. 188; base of Pr inserted into arms of internal ridge (Fig. 130); SBS with larger and smaller lateral spinules (Fig. 282); PPCl as in Fig. 281; other characters and measurements given in Table 5.

SPECIMENS EXAMINED. CUBA: La, Rio Mosquito (Mouth), 22/ 01N, 82/43W, 21-VI-1968, coll. Hruska [ANSP]; La, FAP loc. H or L, 13-XI-1968, coll. Hruska [ANSP]: El Dique, La Habana, 23 01N, 82 14'W, -2La, 1PrP, 8-I-1969; La, 23-IX-1968; 2La (11), 9-IX-1968; 2La, 13-XI-1968, coll. Hruska [ANSP].

Labrundinia sp. 9

This species is unusual in the very narrow head, indistinct maculation (Fig. 107), the truncate base of the Pr (Fig. 126) and the spined claw associated with the PPCl (Fig. 284). Its placment is tentative, it is known from only one speciemen from Colombia

LARVA. Head, ventral view as if Fig. 107; LVS group like that of *L. maculata* (Fig. 138), indistinct; CVS group also barely differentiated (Fig. 160); Li in Fig. 183; apex of MD in Fig. 174; base of Pr truncate as in Fig. 126; AP elongate (Fig. 286); SBS (Fig. 283) with apparently one elongate basal spinule; PPCl (Fig. 284) with some spurs at base and an associated claw with several inner and outer spinules; other characters and measurements given in Table 5.

SPECIMENS EXAMINED. COLOMBIA: La, Pond at Hacienda El Viento, 32km ENE of Puerto Lopez, Dept. del Meta, 10-XII-1969, coll. Roback [ANSP].

Group D

PUPA. RO globose (Fig. 66); ANi distinct (Figs. 66, 67); AeT elongate, convoluted (Fig. 67); preapical groove of RA not evident; abdominal tergites III-VII, humped (Fig. 15)

SPECIES. *L.* sp. 10.

DISTRIBUTION. S.E., U.S.

This group is represented by two specimens of a very distinctive pupa. This pupa has to-date not been associated with any larva or adult. There is a possibity that it could be associated with *L.* sp. 6 of Group C. The pupae of the latter group are unkown. The thoracic comb (Fig. 1) superficially resembles that of the *L. virescens* group (Fig. 2). The pupae of Group D and the *L. virescens* group have dorsal humps on the abdominal tergites III-VII (Fig. 15).

Labrundinia sp. 10

This species is represented only by two PEx specimens from Georgia. The structure of the AeT (Fig. 67) is unique. In other respects they resemble the pupae of the *L. virescens* group.

PUPA. RO as in Fig. 66; detail of ANi with convoluted AeT (Fig. 67); no preapical groove evident; thoracic comb as in Fig. 1; setae and hump of A.IV in Fig 15; caudolateral tubercle of A.IV as in Fig. 17; A.VIII, AL of male shown in Fig. 94; detail of dorsal shagreen on A.VII in Fig. 12; other characters and measurements given in Table 8.

SPECIMENS EXAMINED. GEORGIA: mPEx, Ochlocknee R. at State Rt. 1943, Colquitt Co., 19-IX-1984, coll. Caldwell [ANSP]; fPEx, Little Attapulgus Cr., 0.9 mi S. State Rt. 1952, Decatur Co., 10-VIII-1983, coll. Caldwell [GDNR].

Group E

PUPA. RO short with long curved preapical groove (Fig. 68); partial caudomesal groove present (Fig. 69); spinules on AL small (Fig. 72); plastron plate relatively large (Fig. 70).

SPECIES. *L.* sp. 11.

Table 5. Comparison of range of measurements (µ) and ratios for larvae of *Labrundinia* group C. Numbers in [ ] = n for means. A = absent, P = present

	L. sp 6 [4]		L. sp. 7 [3]		L. sp. 8 [4]		L. sp. 9
	r	mean	r	mean	r	mean	
H-pustules	-P	-	-P	-	-P	-	P
H-Mac.C	-A	-	-A	-	-A	-	A
H-Mac. V	-P	-	-P	-	-P	-	P
H-LVS	-5	-	-	-	5-6	5.5[2]	4
H-CVS	-4	-	4-5	4.5[2]	4-5	4.5[2]	8+
A_1-L	204-241	227.8	192-196	193.3	211-222	2.173	192
A_2-L	73-77	75.52	51-53	51.7	-60	-	83
AR	2.52-2.93	2.748	3.05-3.50	3.217	-3.3	-	2.06
MD-L	90-91	90.8	86-88	86.7	82-91	86.8	76
ApT-L/W	3.60-3.78	3.659[3]	-3.27	-	3.09-3.20	3.145[2]	2
ApT/MD	0.26-0.29	0.273[3]	-0.29	-	0.27-0.32	0.293[5]	0.26
A_1/MD	2.24-2.65	2.508	2.18-2.28	2.230	2.44-2.66	2.508	2.53
P_1L	34-35	34.3[3]	31-37	24.0	31-34	32.3[3]	31
P_1L/W	3.83-4.18	4.003[3]	3.82-4.55	4.183[3]	4.18-4.40	4.253[3]	4.2
CS,P_1	0.88-0.91	0.895[2]	0.84-0.87	0.857	-0.81	-	0.86
A_1/.P_1	6.74-7.09	6.867[3]	5.19-6.19	5.713	6.53-7.03	6.790[3]	6.19
Li-L(O)	58-63	60.3	53-58	56.0	51-58	53.0[3]	50
It/O	0.93-0.96	0.943	0.92-0.93	0.927	0.89-0.94	0.920[3]	0.94
Mt/O	0.95-0.98	0.973	0.97-0.99	0.980	0.97-1	0.985[2]	1.03
Pl-L	-29	-	25-26	25.5[2]	-31	-	26
no. teeth PH	6-6	6.0[2]	6-6	6.0	-7	-	6
Pc-L	196-218	208.3[3]	174-178	175.3	170-185	178.7[3]	118
Pc-L/W	5.70-5.90	5.830[3]	5.88-6.4	6.183	6.13-7.54	6.640[3]	4.57
PPCl-A	58-61	59.5[2]	44-50	49	58-64	60.7[3]	70
PPCl-B	95-95	95.0[2]	77-88	81.7	77-88	81.7[3]	105
PPCl-C	107-108	107.5[2]	101-127	109.7	95-102	98.7[3]	97
B/C	0.88-0.89	0.885[2]	0.70-0.79	0.750	0.78-0.86	0.827[3]	1.08
access dk. cl.	A	-	A	-	A	-	A

DISTRIBUTION. Trinidad.

This group is in some respects intermadiate between the *L. pilosella* and *L. virescens* group. The general shape and size of the RO is similar to the *L. pilosella* group as are the small spinules of the AL. The curved upper portion of the RA creates a long preapical groove and a small caudomesal groove— the overall RA approaches the S-shaped RA of the *L. virescens* group. The plastron plate (Fig. 70) is the largest of any known *Labrundinia* species.

Labrundinia sp. 11

PUPA. RO as in Fig 68; upper portion of RA curved, forming long preapical and small caudomesal grooves (Fig. 69); plastron plate 16 long (Fig. 70); L/W 1.37; AeT relatively short; thorax and WP pale brown; abdomen marked as in *L. pilosella* (Fig. 13); scar A.I as in Fig. 71; mesal humps of tergites only faintly indicated; placement of LS.VII,VIII and AL shown in Fig. 72; other characters and measurements given in Table 7.

SPECIMENS EXAMINED.TRINIDAD: fPEx, Guanapo River, 15-I-1977, coll. Coffman [COFF].

Unknown Placement

Labrundinia sp. 12

This species represented by a pair of poor pupae, cannot be clearly placed. Both lack the RO and except for the unusual abdominal maculation (Fig. 77) are not differentiable from species of the *L. pilosella* or *L. maculata* groups. The maculation resembling that of some *Ablabesmyia* species is probably derived from that shown for *L. pilosella* (Fig. 13). Fig. 77 and the data given in Table 7 will suffice to define this taxon for the present.

SPECIMENS EXAMINED. TRINIDAD: mPEx, Oropuche River, 15-I-1977, coll. Coffman [COFF;] mPEx, Marianne River, 15-I-1977, coll. Coffman [COFF].

DISTRIBUTION

The genus *Labrundinia* appears to be primarily a new world genus. There are at least eight species in North America. Except for the *L. pilosella* group they are mostly Eastern or Southeastern U.S. in distribution. This paper records at least five species from Colombia and two species each from Cuba, Trinidad and Venezuela. There appear to be numerous undescribed species from the neotropics. I have seven underscribed adults from Colombia in the ANSP collections. *L. longipalpis* (Goetg.) is the only European species described to-date. Freeman and Cranston (1980) do not record any species from the Afrotropical Region nor do Sublette and Sublette (1973) record any from the Oriental Region. None have been recorded from New Zealand or Australia by Freeman (1959, 1961) or Roback (1982a, b). One larva recorded by Zavřel (1933) from Sumatra as *Pentaneura* sp. could be either a *Labrundinia* or *Nilotanypus*. Inasmuch as *Nilotanypus* is known from India (Roback 1986) and Japan (Tokunaga 1937) it most probably belongs to the latter genus.

ECOLOGY AND CHEMISTRY

The larvae and pupae of *Labrundinia* are found in a variety of bodies of water from small clear streams to lakes and bays. In general they prefer slower water and in many flowing streams they are found in the backwater, slower, portions of the stream or in other streams with no visible flow. They are common in small ponds and lakes and the European *L. longipalpis* (Goetg.) is primarily a bay-dweller. In most cases, *Labrundinia* larvae are bottom dwellers either in mud or mud-sand mixtures. One exception is *L. pilosella* which I have collected and reared from willow root masses trailing in the Savannah River. These root masses are filled with silt and internally are not affected by the river flow.

There is insufficient data to give meaningful chemical parameters for individual species but overall they have been found at a total hardness

Table 6. Comparison of range of measurements (μ) and ratios for pupae of *L. pilosella* and *L. maculata* group. Numbers in [ ] = n for means.

	L. pilosella [10]		L. becki [3]		L. maculata [7]		L. sp. 1 [2]	
	r	mean	r	mean	r	mean	r	mean
RO-L	202-268	222.3	200-211	204.3	211-269	239	252-255	253.5
RO L/W	2.47-3.13	22.774	2.63-3.00	2.873	1.86-2.78	2.221	2.38-2.42	2.40
AeT-L	13-18	14.0	15-17	15.7	12-24	17.4	20-28	24.0
A.VII-L	192-270	234.7	192-200	196	192-233	209.1	215-244	229.5
pos. LS_1	0.41-0.49	0.447	0.33-0.42	0.367	0.30-0.44	0.390	0.37-0.43	0.400
pos. LS_2	0.54-0.62	0.573	0.48-0.53	0.497	0.47-0.56	0.515	0.50-0.53	0.515
pos. LS_3	0.71-0.77	0.746	0.67-0.72	0.693	0.69-0.75	0.727	0.68-0.72	0.700
pos. LS_4	0.90-0.96	0.937	0.90-0.96	0.923	0.90-0.95	0.923	0.86-0.90	0.880
A.VIII-L	126-196	168.3	122-140	131.7	137-163	148.5	141-166	153.5
pos. LS_1	0.19-0.29	0.256	0.21-0.24	0.223	0.22-0.29	0.254	0.29-0.34	0.320
pos. LS_2	0.40-0.51	0.464	0.39-0.47	0.427	0.42-0.52	0.471	0.47-0.53	0.500
pos. LS_3	0.62-0.71	0.662	0.61-0.63	0.617	0.61-0.70	0.660	0.67-0.74	0.705
pos. LS_4	0.79-0.86	0.824	0.78-0.79	0.787	0.79-0.86	0.821	0.80-0.87	0.835
pos. LS_5	0.93-0.98	0.961	0.94-0.95	0.943	0.95-0.98	0.861	0.93-0.97	0.950
AL-L	237-296	280.9	252-270	260.3	222-300	258.1[8]	278-281	279.5
AL-L/W	2.69-3.57	3.064	3.33-3.65	3.52	2.96-3.52	3.192[6]	3.04-3.12	3.080
pos. LS_1AL	0.33-0.40	0.359[9]	0.31-0.40	0.36	0.33-0.47	0.407	-0.42	-
pos. LS_2AL	0.46-0.53	0.493[9]	0.45-0.53	0.493	0.45-0.53	0.566	-0.52	-
AL-no. spurs	7-10	8.8	9-11	10	6-11	8.7	-9	-
AL longest spur	6-10	7.5	8-9	8.7	6-11	9.5	-6	-
male GS/AL	1.04-1.13	1.075[4]	0.95-1	0.975[2]	0.90-0.97	0.938[5]	0.96	-
female GS/AL	0.27-0.32	0.294[5]	-0.31	-	0.31-0.32	0.320[2]	-0.33	-

Table 7. Comparison of measurements (μ) and ratios for pupae of *L. neopilosella* group, L. group E and unknown group (sp. 12). Numbers in [ ] = n for means.

	L. neopilosella [4]		L. neopilosella var. 1	L. johannseni [2]		L. sp. 11	L. sp. 12
	r	mean		r	mean		
RO-L	192-250	222.0	264	237-269	253.0	192	-
RO L/W	1.96-2.23	2.102	2.04	2.13-2.37	2.260	2.60	-
AeT-L	29-32	30.8	31	19-20	19.5	15	-
A.VII-L	192-215	206.3	259	233-421	237.0	185	204
pos. LS_1	0.36-0.44	0.408	0.47	0.46-0.49	0.475	0.48	0.38
pos. LS_2	0.50-0.54	0.53	0.54	0.56-0.58	0.570	0.58	0.53
pos. LS_3	0.70-0.75	0.725	0.74	0.71-0.78	0.745	0.76	0.69
pos. LS_4	0.92-0.97	0.945	0.93	0.95-0.95	0.950	0.92	0.89
A.VIII-L	141-159	149.0	185	167-178	172.5	148	130
pos. LS_1	0.24-0.28	0.255	0.26	0.21-0.27	0.240	0.3	0.26
pos. LS_2	0.41-0.54	0.465	0.48	0.46-0.49	0.475	0.48	0.43
pos. LS_3	0.53-0.72	0.650	0.68	0.67-0.69	0.680	0.65	0.66
pos. LS_4	0.79-0.87	0.825	0.84	0.84-0.85	0.845[2]	0.85	0.8
pos. LS_5	0.92-0.98	0.963	0.96	0.98-0.98	0.980	0.95	0.97
AL-L	241-263	254.5	300	278-289	283.5	226	255
AL-L/W	2.95-3.46	3.183	3.68	-3.88	-	3.05	3.63
pos. LS_1AL	0.36-0.42	0.395	0.4	0.4-0.4	0.400	0.3	0.32
pos. LS_2AL	0.47-0.52	0.498	0.49	0.51-0.51	0.510	0.43	0.45
AL-no. spurs	8-10	9.0	8	7-9	8.5	6	8
AL longest spur	9-13	11.0	8	7-10	8.5	5	10
male GS/AL	-	-	0.96	-0.9	-	-	1.07
female GS/AL	0.28-0.32	0.295	-	-0.31	-	0.31	-

Table 8. Comparison of measurements (µ) and ratios for pupae of *L. virescens* group and L. group D. Numbers in [ ] = n for means.

	L. virescens [4]		L. sp. 3 nr. virescens [4]		L. sp. 3	L. sp 10 [2]	
	r	mean	r	mean		r	mean
RO-L	240-240	240.0[2]	255-288	271.5[2]	-	374-394	384.0
RO L/W	1.72-1.79	1.755[2]	2.23-2.31	2.270[2]	-	1.48-1.64	1.560
AeT-L	38-39	38.5[2]	34-41	37.3	-	sinuate	
A.VII-L	226-286	261.7	218-303	264.5	-	270-296	283.0
pos. LS_1	0.26-0.35	0.303	0.36-0.44	0.408	-	0.34-0.40	0.370
pos. LS_2	0.38-0.47	0.427	0.46-0.54	0.513	-	0.38-0.54	0.460
pos. LS_3	0.62-0.69	0.653	0.71-0.74	0.725	-	0.68-0.74	0.710
pos. LS_4	0.94-0.97	0.953	0.88-0.94	0.910	-	0.95-0.95	0.950
A.VIII-L	181-204	190.0	159-207	188.7	-	200-207	203.5
pos. LS_1	0.240.29	0.263	0.28-0.33	0.305	-	0.36-0.37	0.365
pos. LS_2	0.45-0.49	0.473	0.50-0.58	0.523	-	0.57-0.61	0.590
pos. LS_3	0.64-0.67	0.653	0.67-0.71	0.703	-	0.73-0.78	0.755
pos. LS_4	0.80-0.84	0.818	0.84-0.87	0.853	-	0.86-0.86	0.860
pos. LS_5	0.94-0.96	0.953	0.95-0.98	0.963	-	0.96-0.98	0.970
AL-L	385-392	388.7	289-355	322	223	344-370	357
AL-L/W	3.59-4.04	3.763	2.89-3.42	3.063	3.75	3.24-4.00	3.620
pos. LS_1AL	0.24-0.29	0.267	0.29-0.35	0.313	0.31	0.38-0.39	0.385
pos. LS_2AL	0.33-0.37	0.353	0.41-0.48	0.440[3]	0.45	0.45-0.48	0.465
AL-no. spurs	11-14	12.7	7-9	8.5	7	11-14	12.5
AL longest spur	29-31	30.3	15-19	17.0	24	12-12	12.0
male GS/AL	-1.03	-	-1.3	-	-	-0.96	-
female GS/AL	-0.25	-	0.26-0.29	0.275[2]	0.33	-0.27	-

of 14-94 ppm (Ca 8-92, Mg 2-8), alkalinity ppm (MO) 0-82, specific conductivity μhos at 25° C) 48-197, pH 4.5-7.2 (most around 7.0), temp. 19-24C, alt. 100-300'.

Dr. Ferrington has kindly furnished me with the data for *L. maculata* which (at least in Kansas) lives in an unusual body of water (Short Creek) with high heavy metal concentrations. The average figures given in parentheses represent at least four seasonal values pH 6-8.2, alk. 8.0-18.4 (14.28 mg/l); spec. cond. 461-565 (528); total diss. solids 368-403 (391 mg/l); barium 23-34 (29.3 μg/l); cadmium 110-170 (125 μg/l); manganese 150-1700 (127.5 μg/l); zinc 16,000-25,000 (18,750 μg/l); NO_2- NO_3 0.33-3.14 (1.33 mg/l); total phosphorus 0.36-1.21 (0.66mg/l); potassium 2.6-5.0 (3.50 mg/l);

LITERATURE CITED

Beck, W. M. and E. C. Beck. 1966. Chironomidae (Diptera) of Florida I. Pentaneurini (Tanypodinae). Bulletin of the Florida State Museum. Biological Series 10(8): 305-379.

Coffman, W. P. 1983. Thoracic chaetotaxy of chironomid pupae (Diptera: Chironomidae). Memoirs of the American Entomological Society 34: 61-70.

Fittkau, E. J. 1962. Die Tanypodinae (Dipetra: Chironomidae). Abhandlungen zur Larvalsystematik der Insekten. 6: 453 pp.

Fittkau, E. J. and D. A. Murray. 1986. The pupae of Tanypodinae (Diptera: Chironomidae) of the Holarctic Region. *In* : Wiederholm, T. Chironomidae of the Holarctic Region. Entomologica Scandinavica Supplement No. 28:31-113.

Fittkau, E. J. and S. S. Roback. 1983. The larvae of Tanypodinae (Diptera: Chironomidae). *In:* Wiederholm, T. Chironomidae of the Holarctic Region. Entomologica Scandinavica Supplement No.19: 33-110.

Freeman, P. 1959. A study of New Zealand Chironomidae (Diptera: Nematocera) Bulletin of the British Museum (N.H.) Entomology London 7: 396-437.

Freeman, P.. 1961. The Chironomidae (Diptera) of Australia. Australian Journal of Zoology 9:611-737.

Freeman, P. and P. S. Cranston. 1980. Family Chironomidae, In Catalogue of the Diptera of the Afrotropical Region. The British Museum (N.H): 175-202.

Kowalyk, H. E. 1985. The larval cephalic setae in the Tanypodinae (Diptera: Chironomidae) and their importance in generic determinations. The Canadian Entomologist 117: 67-94.

Lenat, D. 1984. Revision of *Labrundinia*, keys. Southeastern Water Pollution Biologists Association Newsletter, V.8 No. 3

Loew, H. 1866. Diptera Americae Septentrionalis, Centuria Septima. Berliner Entomologische Zeitschrift 10: 1-54.

Roback, S. S. 1971. The adults of the subfamily Tanypodinae (=Pelopiinae) in North America (Diptera: Chironomidae). Monographs of the Academy of Natural Sciences of Philadelpha 17: 410 pp.

Roback, S. S. 1974. The immature stages of the genus *Coelotanypus* in North America. Proceedings of the Academy of Natural Sciences of Philadelphia 126: 9-19.

Roback, S. S. 1976. The immature chironomids of the Eastern United States I. Introduction and Tanypodinae-Coelotanypodini. Proceedings of the Academy of Natural Sciences of Philadelphia 127: 147-201.

Roback, S. S. 1977. The immature chironomids of the Eastern United States II. Tanypodinae-Tanypodini. Proceedings of the Academy of Natural Sciences of Philadelphia 189: 55-87.

Roback, S. S. 1978. The immature chironomids of the Eastern United States III. Tanypodinae-Anatopyniini. Macropelopiini and Natarsiini. Proceedings of the Academy of Natural Sciences of Philadelphia 129: 151-202.

Roback, S. S. 1980. The immature chironomids of the Eastern United States IV. Tanypodinae-Procladiini. Proceedings of the Academy of Natural Sciences of Philadelphia 132: 1-63.

Roback, S. S. 1981. The immature chironomids of the Eastern United States V. Pentaneurini-*Thienemannimyia* group. Proceedings of the Academy of Natural Sciences of Philadelphia 133: 73-128.

Roback, S. S. 1982a. The immature stages of some Australian Tanypodinae (Diptera), with some notes on the adults. Journal of the Australian Entomological Society 21:147-160.

Roback, S. S. 1982b. The Tanypodinae (Diptera: Chironomidae) of Australia II. Proceedings of the Academy of Natural Sciences of Philadelphia 134: 80-112.

Roback, S. S. 1985. The immature chironomids of the Eastern United States VI. Pentaneurini - Genus *Ablabesmyia* . Proceedings of the Academy of Natural Sciences of Philadelphia 128: 49-54.

Roback, S. S. 1986a. The immature chironomids of the Eastern United States VII. Pentaneurini-Genus *Monopelopia* with redescription of the male adults and description of some Neotropical material. Proceedings of the Academy of Natural Sciences 138(2): 350-365.

Roback, S. S. 1986b. .The immature Chironomids of the Eastern United States VIII. Pentaneurini-Genus *Nilotanypus* with the description of a new species from Kansas. Proceedings of the Academy of Natural Sciences of Philadelphia 138(2): 443-465.

Roback, S. S. and W. P. Coffman. 1977. New records of probable *Djalmabatista* pupae from Eastern North America and Venezuela (Chironomidae: Tanypodinae). Proceedings of the Academy of Natural Sciences of Philadelphia 128: 49-54.

Roback, S. S. and W. W. Moss. 1978. Numerical taxonomic studies on the congruence of classifications for the genera and subgenera of Macropelopniini and Anatopyniini (Diptera: Chironomidae: Tanypodinae). Proceedings of the Academy of Natural Sciences of Philadelphia 129: 125-150.

Roback, S. S. and K. J. Tennessen. 1978. The immature stages of *Djalmabatista pulcher* [= *Procladius* (*Calotanypus*) *putcher* (Joh.)]. Proceedings of the Academy of Natural Sciences of Philadelphia 126: 12-23.

Saether, O. A. 1980. Glossary of chironomid morphology terminology (Diptera: Chironomidae). Entomologica Scandinavica, Supplement 14: 51 pages.

Sublette, J. E. and M. Sublette. 1973. Family Chironomidae. Pages 389-422 *In:* M. D. Delfinado and D. E. Hardy. A Catalogue of the Diptera of the Oriental Region. Volume 1. suborder Nematocera. The University Press of Hawaii, Honolulu.

Tokunaga, M. 1937. Chironomidae from Japan (Diptera) IX. Tanypodinae and Diamesinae. Philippine Journal of Science 62: 21-65.

Zavřel, J. 1932. Larven und Puppen der Tanypodinen von Sumatra and Java. Archiv fur Hydrobiologie Supplement-Band XI: 604-624.

Proceedings of The Academy of Natural Sciences of Philadelphia 139: 211-221, 1987

New Species of *Labrundinia* from Colombia (Diptera: Chironomidae: Tanypodinae)

SELWYN S. ROBACK
Department of Entomology, The Academy of Natural Sciences of Philadelphia
19th and the Parkway, Philadelphia, PA 19103

ABSTRACT.— Seven new species of the genus *Labrundinia* are described from the Llanos of Colombia. These are *L. tenata*, *L. parabecki*, *L. fera*, *L. opela*, *L. fosteri*, *L. meta* and *L. hirsuta*. A preliminary key to the male adult stage of the genus *Labrundinia* from the New World is offered. [Chironomidae Colombia, key to males, *Labrundinia*, new species, Tanypodinae]

The seven new species of *Labrundinia* described in this paper were collected, at light, on the Hacienda Mozambique in the Dept. del. Meta in Colombia. They were collected in 1971 and 1972 by the author and Dr. Neal R. Foster (U.S. Fish & Wildlife Service, Ann. Arbor). A detailed description of the area and especially the Laguna Mozambique is given in Roback and Nieser (1972). Unfortunately none of the adults here described could be associated with the larvae described from this area in Roback (1987). It is difficult to place these adults in the species groups (based primarily on larval and pupal characters) suggested in Roback (1987). *L. parabecki* n. sp. would probably fall in the *L. pilosella* group while *L. opela* n. sp. and *L. hirsuta* might belong in the *L. virescens* group. The Neotropical species demonstrate a few characters not usually present in the Neacrtic and Palaearctic species of *Labrundinia*. These are bifid male claw present in some species (Fig. 18); the *Larsia*-like tibial spurs with a total of three to four teeth on Ti I (Fig. 5, 6) and three or five teeth on Ti II (Figs. 7, 8); the occasionally banded wings (Figs. 39, 40), the distinct presence of R_{2+3} (Figs. 3,4); the supraalar callus with two to three setae; the occasional presence of a distinct anterior spur on strut 3 (Figs. 33, 36, 37) of the male genitalia (coxosternapodeme of Saether, 1980). There is nothing in these adult male characters to indicate that any subdivisions of the genus *Labrundinia*, other than the species groups suggested in Roback (1987), are needed.

All specimens are in the entomological collections of the Academy of Natural Sciences of Philadelphia.

The following abbreviations are used in the text and tables. With some few exceptions they follow Saether (1980).

AR	antennal ratio
A.I-IX	abdominal segments
Co.	color
CS	campaniform sensillum
F	femur
Fl_{1-14}	antennal flagellomeres
Gc	gonocoxite
Gs	gonostylus
HR,	hypopygium ratio, Gc/Gs
L,	length
LR	leg ratio
Ta_{1-5}	tarsal segment
Ti	tibia

T.IX	ninth abdominal tergite
W	width
WL	wing length, arculus to tip
I-III	pro-, meso-, metathoracic legs

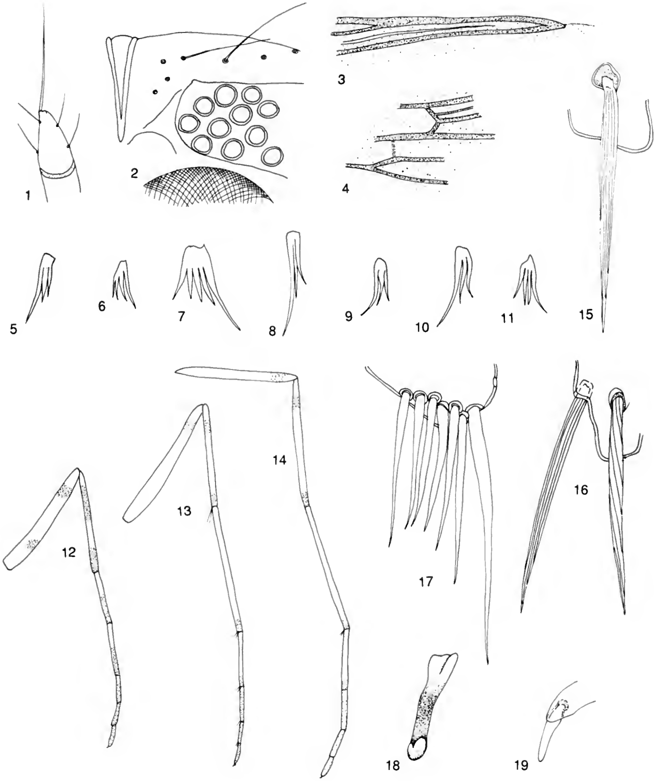
KEY TO NEW WORLD ADULT MALES

Inasmuch as so few specimens are involved in the descriptions of the North American as well as in the Colombian *Labrundinia* species, the following key must be considered to be provisional in nature. It attempts to include all the New World *Labrundinia* species known to me. The data in Tables 1 and 2 as well as the figures will serve to aid in the separation of the Colombian species. The color patterns of the Nearctic species are illustrated in Roback (1971). Edwards (1931) stated that *Pentaneura separata* Edw. is related to *L. longipalpis* (Goetg.) The description appears close to *Labrundinia* but differs in that Costa ends distinctly before the level of Cu_1. If it is a *Labrundinia*, it would key close to *L. parabecki* n. sp. (couplet 6). Fittkau (1962) cites some undescribed material collected by Brundin (4 sp. from North America and Mexico, 3 sp. from South America) and a species collected by Sioli from the Amazon area.

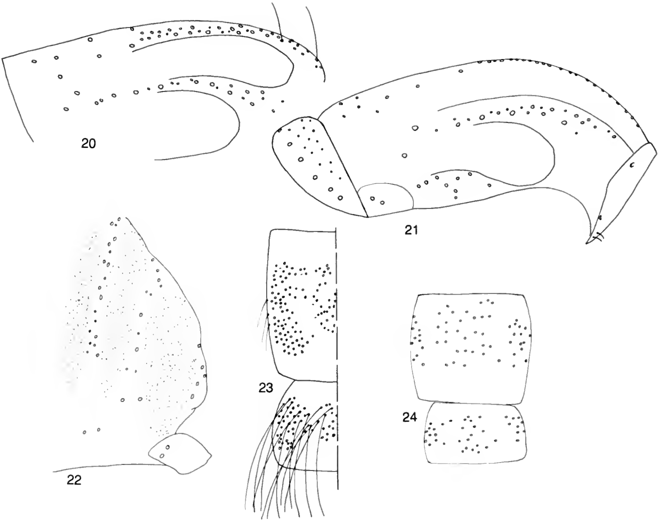
1. A.I, II wholly pale (Figs. 29-31); at most only a pair of faint spots on A.II (Fig. 30) and a trace on A.I 2
- A.I pale to brown (Figs. 25-28); A.II with a divided band (Fig. 28), a complete band, not >0.25 segment length (Figs. 25, 27) or wholly brown (Fig. 26) 5
2. A.II and V with only faint spots; A.VIII pale (Fig. 30) .... *L. meta* n. sp.
- A.II with only faint spots to wholly clear (Figs. 29, 31); A.V with a distinct band (Figs. 29, 31); A.VIII dark 3
3. A.V with narrow, laterally tapering band (Fig. 31); A.VI with U-shaped band; hairs on A.VII, VIII (Fig. 23) very dark and dense, tend to cover Gc .... *L. hirsuta* n. sp.
- A.V with about 0.50 segment, brown (Fig. 29); A.VI almost wholly brown (Fig. 29); hairs on A.VII, VIII less dense (Fig. 24) 4
4. A.V about 0.50 brown (Fig. 29); A.VI about 0.66 brown (Fig. 29) .... *L. opela* n. sp.
- A.V over 0.75 brown; A.VI almost wholly brown .... *L. virescens* Beck & Beck
5. Abdomen (Fig. 26) and genitalia (Fig. 33) wholly brown 6
- Abdomen with any or all of segments II-VI with basal bands (Figs. 25, 27, 28); genitalia variable 7
6. A.II-IV with darker cruciate marks (Fig. 26); LR I 0.75 .... *L. parabecki* n. sp.
- A.II-IV more uniform in color; LR I 0.55 .... *L. becki* Roback
7. Gc pale to slightly infuscated (Fig. 3) 8
- Gc with apical 0.50 brown (Fig. 34) to wholly brown (Fig. 32) 12
8. Band on A.II broken in to three spots; bands on A.III, IV subequal with darker spots (Fig. 28); wing appears to have two bands.. *L. fosteri* n. sp.
- Band on A.II continuous; apices of bands may be very irregular; no wing bands 9
9. Bands on A.II-IV subequal in depth .... *L. neopilosella* Beck & Beck
- Band on A.III distinctly deeper than those on A.II and IV 10
10. Band on A.III>0.50 segment length; slightly deeper than those on A.II and IV .... *L. maculata* Roback
- Band on A.III fill most of segment; more than 2x as deep as bands on A.II and IV 11
11. Bands on A.II and IV sharply demarcated from pale background; A.VI almost wholly brown .... *L. johannseni* Beck & Beck
- Bands on A.II and IV not as sharply demarcated from infuscated segments; A.VI band similar to Fig. 27 .... *L. pilosella* (Loew)
12. Gc with apical 0.50 brown (Fig. 34) with long pale apical hairs; abdominal maculation as in Fig. 27 .... *L. fera* n. sp.
- Gc wholly brown (Fig. 32); abdominal maculation as in Fig. 25 .... *L. tenata* n. sp.

The following characters are common to all the species here described and need not be repeated in each description.

(1) Head brown; (2) orbitals to upper third of dorsal eye extension, uniseriate, forming slight angle above eye (Fig. 2); (3) diameter of pedicel subequal to interocular space; (4) CS present



FIGS. 1-19. 1, Fl$_{14}$, *L. hirsuta*; 2, orbitals and dorsal eye extension, tenata; 3, apex of radial sector, wing, *L. hirsuta*; 4, base of radial sector, r-m and m-cu, wing, *L. hirsuta*. 5-11: tibial spurs. 5, Ti II, *L. tenata*; 6, Ti I, *L. parabecki;* 7, Ti II, *L. parabecki*; 8, Ti II, *L. fera*; 9, Ti I, *L. fosteri;* 10, Ti II, *L. fosteri;* 11, Ti I, *L. hirsuta*. 12-14, legs, *L. fosteri*; 12, leg I; 13., leg II; 14, leg III; 15, pseudospur Ta$_1$ III, *L. tenata*; 16, pseudospurs Ta$_1$ II, *fosteri*; 17, comb Ti III, *meta*; 18, claw, ventral view, *L. hirsuta;* 19, megaseta of Gs, *L. meta*.



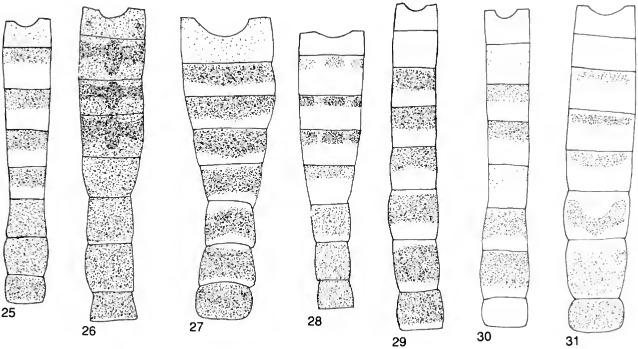
FIGS. 20-24. 20, laterodorsal scutum, *L. fera;* 21, lateral scutum, antepronotum, supraalar callus and scutellum, *L. meta;* 22, dorsal scutum and supraalar callus, *L. tenata;* 23, setal pattern dorsal, A.VII, VIII, *L. hirsuta;* 24, setal pattern, dorsal, *L. tenata.*

ventrally near base of palpal segment 3; (5) antepronotum pale; (6) vittae brown to black-brown, indistinct except in *L. tenata* (Fig. 22); (7) anepisterna and preepisternum brown to black infuscated; (8) achrostichals and dorsocentrals irregular bi-triseriate; two- three sizes of setae (Figs. 20-22); (9) scutellum pale to slightly infuscated; (10) postnotum brown to black; (11) wing densely haired; (12) costa not past R_{4+5} ends at level of Cu_1; (13) distance from m-cu to r-m about 2 x length of m-cu (Fig. 4);

Labrundinia tenata n. sp.

The wholly brown genitalia (Fig. 32) and the partially pale A.II-V (Fig. 25) will separate this species from *L. becki* and *L. parabecki* [wholly dark abdomen (Fig. 26)]. Some specimens of *L. pilosella* possess dark genitalia but A.III, V are wholly brown in that species (Roback 1971, Figs. 540, 541).

Adult male.—Pedicel with one lateral and two ventral setae; orbitals and dorsal eye extension as in Fig. 2; AR 1.20; Fl_{14} as in Fig. 1; maxillary palpal segments 2-5 in ratio 37, 89, 196, 204 µ.



FIGS. 25-31. Abdominal color pattern: 25, *L. tenata;* 26, *L. parabecki*; 27, *L. fera*; 28, *L. fosteri*; 29, *L. opela*; 30, *L. meta*; 31, *L. hirsuta.*

Antepronotum with two ventral setae (Fig. 21) and two tubercles as in Fig. 21; dorsocentrals, separated from caudal acrostichals (Fig. 22); two prescutellars; humeri paler, infuscated; four- five humerals (Fig. 22); postalar area slightly paler with five- six postalars; supraalar callus dark with two setae; scutellum with eight scutellars across disc and numerous fine anterior setae.

Leg measurements and ratios in Table 1; F I pale; Ti I pale; Ta_{1-5} I pale infuscated; F II, Ti II and Ta_{1-5} II pale; F III pale; Ti III pale, apex infuscated; Ta_{1-5} III pale; hairs on Ti I short subequal to mesal diameter; hairs on Ti II, III about 12x mesal diameter; claws appear sharp but may be unevenly bifid as in Fig 18; pseudospur (Fig. 15) present on Ta_{1-4} II; none on Ta_{1-4} I or III; long apical spines on Ti II, about 204 μ L; spur Ti I, 13 μ with three teeth (Fig. 5); spur Ti II with three teeth similar to Fig. 5; comb of Ti III with seven setae.

Wing 1.07-1.12 mm L; m-cu 0.29 arculus to wing tip; no wing bands present; base of Rs, r-m and m-cu as in Fig. 4; R_{2+3} not discernable.

Abdominal maculation in Fig 25; T.IX arched, distally banded, with 8-10 setae; Gc wholly brown (Fig. 32); Gc 95-102 μ L; Gc L/W 1.63; HR 1.43-1.53; Gs 64-66 μ L; megaseta of Gs as in Fig. 19, 13 μ L; hairs of A.VII, VIII, more short and scattered (Fig. 24); apical hairs of Gc not numerous, pale brown, about 185 μ L; anterior margin of strut 3 smoothly rounded, no distinct spur (Fig. 32).

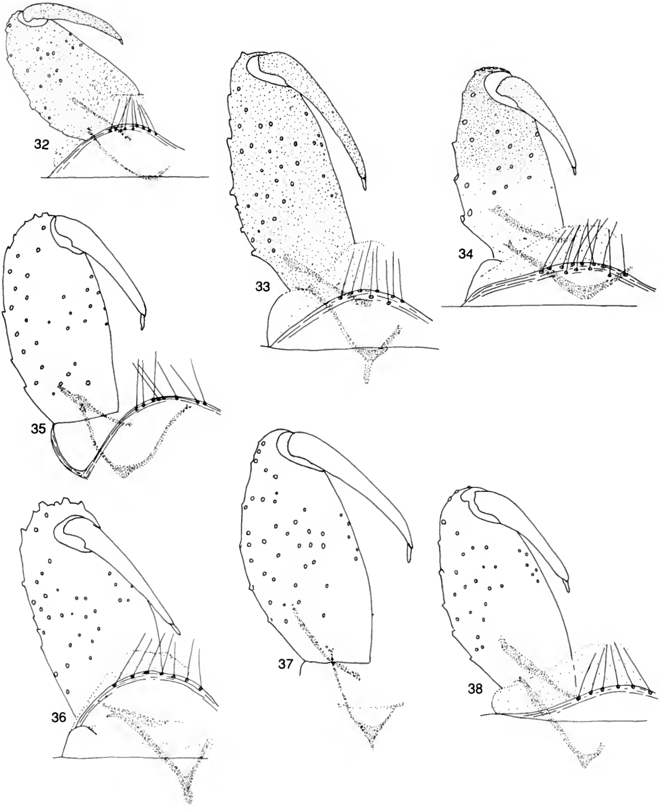
Holotype male.—Laguna Mozambique, 16 km. S.W. of Puerto Lopez, Dept. del Meta, Colombia 25-II-1972, coll. Foster.

Paratypes.— 2 males, same data.

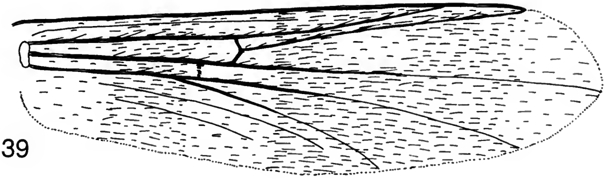
2 males.— Same locality, 9-III-1971, coll. Roback

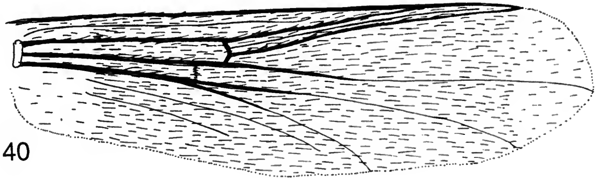
Labrundinia parabecki n.sp.

This is the only species found in Colombia with a wholly brown abdomen and genitalia. The key characters (couplet 6) will separate it from the



FIGS. 32-38. Male genitalia, dorsal; 32, *L. tenata;* 33, *L. parabecki;* 34, *L. fera;* 35, *L. opela;* 36, *L.* *L. hirsuta;* 37, *L. fosteri;* 38, *L. meta.*





FIGS. 39-40. Wings: 39, *L. fosteri*; 40, *L. hirsuta*.

North American *L. becki*.

Adult male.—Pedicel with one lateral and three ventral setae; AR 1.25-1.35; FL_{14} as in Fig. 1; maxillary palpal segments 2-5 in ratio 52, 104, 152, 218 μ; clypeus with 17 long setae.

Antepronotum with five-six antepronotals and two tubercles as in Fig. 21; dorsocentrals extend to caudal end of acrostichals as in Figs. 20, 21, two-four prescutellars present; humeri with pale infuscation; 10 humerals present; postalar area paler with 11-12 setae; supraalar callus dark with two setae; scutellum infuscated with 11 scutellars across disc and some fine anterior setae.

Leg measurements and ratios in Table 1; F I pale; Ti I pale, apex infuscated; Ta_{1-5} I infuscated; F II pale brown; Ti II pale, apex infuscated; $Ta_{1,2}$ II pale; Ta_{3-5} II infuscated; leg III marked as II; hairs on Ti II, III longer, about 7-9x tibial diameter; male claws may be as in Fig. 18; pair of pseudospurs present on Ta_{1-4} II and Ta_1 III; none on Ta_{1-4} I; long apical spines present on Ti II, III, 141-200 μ L; Ti I spur 13 μ L with three-four teeth (Fig. 6); spur Ti II 23-26 μ L with five teeth (Fig. 7); comb of Ti III with eight setae.

Wing 1.15-1.27 mm L; m-cu 0.27 arculus to tip; no bands present; base of Rs, r-m, m-cu as in Fig. 4; R_{2+3} appears faintly present as in Fig. 3.

Abdominal maculation as in Fig. 26; T.IX arched, distally banded with 7-10 setae; Gc wholly brown (Fig. 33); Gc 146-153 μ L; Gc L/W 2.11-2.33; HR 1.39-146; Gs 105 μ L; megaseta of Gs similar to Fig. 19, 16 μ L; hairs of A.VII VIII moderately dense, pale brown; apical hairs of Gc elongate, pale brown, up to 259 μ L; anterior margin of strut 3 with relatively elongate spur (Fig. 33).

Holotype male.—Laguna Mozambique, 16 km SW of Puerto Lopez, Dept. del Meta, Colombia, 25-II-1972, coll. Foster

Paratype male.—same data.

Labrundinia fera n.sp.

The apically brown Gc (Fig. 34) with its long hairs and the abdominal maculation (Fig. 27) with A.II-VI about 0.75 brown will separate thus species from any known to me.

Adult male.— Pedicel with one lateral and two ventral setae; Fl_{14} similar to Fig. 1; maxillary palpus not measureable.

Antepronotum with two-three ventral setae and two tubercles; dorsocentrals extend to apex of acrostichals (Fig. 20); three- six prescutellars; humeri paler, infuscated; six-seven humerals (Fig. 20); postalar area paler with seven postalars supraalar callus dark with two setae; scutellum with 9-10 setae across disc and some fine anterior setae.

Leg measurements and ratios in Table 1; F I with basal spot and apical half brown; Ti I with base and apical half brown; Ta_{1-2} I infuscated, Ta_{3-5} I pale; F II with apical third brown; Ti II and Ta II infuscated; Ta_{2-5} II pale; F III brown; Ti III with base and apex infuscated; Ta_1 III infuscated; Ta_{2-5} III pale; hairs on Ti I short, subequal to mesal diameter; hairs on Ti II, III longer about 8-10x tibial diameter; claws may be as in Fig. 18; one pseudospur present on Ta_{1-4} II; none appear present on legs I or III; pair of long apical spines on Ti II 141-180 μ L; spur Ti I 13 μ L with three teeth, spur Ti II 20 μ with three teeth (Fig. 8); comb of Ti III with about eight setae similar to Fig. 17.

Wing 1.20 mm L; m-cu 0.26 arculus to tip; wing hairs very dense; no banding present; base of Rs, r-m and m-cu as in Fig. 4; R_{2+3} not visible.

Abdominal maculation as in Fig. 27; T.IX with marginal band and 13 setae; Gc with apical half brown (Fig. 34); Gc and Gs measurements in Table 2; abdominal hairs moderately dense and dark esp. on A.VII, VIII; hairs of Gc elongate, up to 290 μ L; concentrated toward apex, darker basally, paler at apex.

Holotype male.—Laguna Mozambique, 16 km SW of Puerto Lopes, Dept. del Meta, Colombia, 25-II-1972, coll. Foster.

Labrundinia opela n.sp.

This species which appears to belong to the *L. virescens* group (A.I, II pale) differs from *L. virescens* in the narrower bands on A.V, VI (Fig. 29). The darker A.V and VIII will separate it from *L. meta* (Fig. 30) and the general abdominal maculation is distinct from that of *L. hirsuta* (Fig. 31). It also lacks the wing band of *L. hirsuta*.

Adult male.— Pedicel with one lateral and two ventral setae; Fl_{14} similar to Fig. 1; maxillary palpus not measureable.

Anteprontum similar to Fig. 21 with two-three ventral setae and two tubercles; dorscentrals extend to caudal end of acrostichals as in Fig. 20; two-four prescutellars; humeri paler, infuscated; six-seven humerals; postalar area paler with 9-10 postalars; supraalar callus dark with two large setae; eight scutellars across disc with numerous fine setae anterior to these.

Legs with tarsi missing; measurements of F and Ti in Table 1; F and Ti of all legs pale; hairs on Ti I short subequal to mesal diameter; hairs on Ti II, III missing; apical spines Ti II, III missing; spur on Ti I 15 μ L with four teeth similar to Fig 6; spur Ti II 22 μ L; comb of Ti III with six setae.

Wing with m-cu 0.27 arculus to tip; length in Table 2; no bands; base of Rs, m-cu and r-m as in Fig. 4; R_{2+3} appears present as in Fig. 3.

Abdominal maculation in Fig. 29; T. IX with apical brown band and nine setae; Gc pale (Fig. 35); genitalia measurements in Table 2; megaseta of Gs as in Fig. 19, 15 μ L; most hairs of A.I-VIII and Gc missing; A.VII, VIII setal pattern similar to Fig. 24; anterior margin of strut 3 with only a suggestion of an anterior spur (Fig. 35).

Holotype male.—Laguna Mozambique, 16 km SW of Puerto Lopez, Dept. del Meta Colombia, 6-III-1971, coll. Roback.

Labrundinia fosteri n.sp.

Table 1. Leg measurements (μ) and ratios for the new species of *Labrundinia* from Colombia.

	Leg	F	Ti	Tai	Ta2	Ta3	Ta4	Ta5	LR
tenata									
	I	370	363	255	163	118	81	67	0.97
	II	481	370	525	233	111	74	74	1.42
	III	459	500	555	218	141	93	70	1.11
parabecki									
	I	377	403	315	178	130	89	70	0.78
	II	592	451	533	255	148	96	85	1.18
	III	500	544	544	233	167	111	89	1.00
fera									
	I	396	451	289	170	126	100	63	0.64
	II	592	470	555	255	141	100	74	1.18
	III	518	592	570	266	192	122	74	0.96
opela									
	I	370	407	-	-	-	-	-	-
	II	548	418	-	-	-	-	-	-
	III	481	555	-	-	-	-	-	-
fosteri									
	I	444	426	215	204	96	85	67	0.51
	II	648	437	507	204	141	93	81	1.16
	III	500	481	511	233	167	107	81	1.06
meta									
	I	444	463	289	196	126	93	59	0.62
	II	622	385	-	-	-	-	-	-
	III	537	562	555	263	185	111	78	0.99
hirsuta									
	I	481	481	266	189	130	96	63	0.55
	II	629	503	581	259	141	96	78	1.16
	III	537	644	555	274	185	130	78	0.86

Table 2. Some measurements (μ), ratios and characters of the new species of *Labrundinia* from Colombia. BR = brown; P = pale. Where more than one specimen could be measured the mean is given. [ ] = n for mean.

	tenata	parabecki	fera	opela	fosteri	meta	hirsuta
AR	1.20	1.300[2]	1.10	1.34	1.40	1.37	1.565[4]
Gc-L	97.3[3]	149.5[2]	110	126	140.0[2]	125	146.0[3]
Gc-L/W	1.63	2.220[2]	1.88	2.09	2.000[2]	1.94	2.186[3]
Gs-L	65.3[3]	105.0[2]	69	83	98.0[2]	74	88.3[3]
HR	1.480[3]	1.424[2]	1.59	1.52	1.430[2]	1.69	1.653[3]
Gc-Co.	BR	BR	0.5BR	P	P	P	P
WL (mm)	1.090[2]	1.235[2]	1.2	1.19	1.15	1.25	1.290[2]

The nature of the bands on A.II (three spots) A.III-IV (with darker spots) as in Fig. 28, the pale genitalia (Fig. 37) and the two wing bands (Fig. 39) will separate this species from any other *Labrundinia* known. The bands of A.II-V (Fig. 28) differ from those *L. neopilosella, L. maculata* and *L. johannseni* (See Roback 1971, Figs. 535, 545, 546) and none of these species have banded wings. The species is named after my former colleague Dr. Neal Foster who collected the specimens.

Adult male.— Pedicel with one lateral and three ventral setae; antennal ratio in Table 2; Fl_{14} as in Fig. 1, 37μ L; maxillary palpus not measureable.

Anteprotnotum with two ventral setae and two tubercles as in Fig. 21; dorsocentrals irregularly biseriate extend to caudal end of acrostichals as in Fig. 20; three-four prescutellars present; humeri paler, infuscated; six-seven humerals; postalar area infuscated with eight setae; supraalar callus pale with two setae,scutellum with 9-10 scutellars and usual fine setae anteriorly.

Leg measurements and ratios in Table 1; leg maculation in Figs. 12, 13, 14; hairs on Ti I slightly longer than mesal diameter; hairs on Ti II, III about 11x mesal diameter; claws possibly as in Fig. 18; pseudospurs present on Ta_{1-4} II (Fig. 13, 16) and Ta_1 III (Fig. 14); long apical spines on Ti II about 185μ L; Ti I spur (Fig. 9) 13μ L with three teeth; Ti II spur (Fig. 10) 18μ L with three teeth, comb Ti III similar to Fig. 17, six setae.

Wing length Table 2; m-cu 0.26 arculus to tip; two wing bands present formed mostly by dark wing hairs (Fig. 39); one narrow basad of fCu; second extending from base of R to apex of C; base of Rs, r-m, m-cu similar to Fig. 4; R_{2+3} not visible.

Abdominal color pattern in Fig. 28; T.IX with apical brown band and 11 setae (Fig. 28); Gc pale (Fig. 37); Gc 136-144μ; Gc L/W 1.95-2.05; HR 1.36-1.50; Gs 96-100μ; megaseta of Gs similar to Fig. 19, 17μ L; hairs of A.VII, VIII not dense, similar to Fig. 24; apical hairs of Gc, pale, elongate up to 260μ L; most rubbed off; anterior margin of strut 3 with a distinct spur (Fig. 37).

Holotype male.—Laguna Mozambique, 16 km SW of Puerto Lopez, Dept. del Meta, Colombia, 25-II-1972, coll. Foster.

Paratype male.—Same data.

Labrundinia meta n. sp.

The abdominal maculation with T.I clear, T.II, V with only faint spots (Fig. 30) and the pale T.VIII will separate this species from any to-date described. It may possibly belong to the *L. virescens* group.

Adult male.— Pedicel with one lateral and four ventral setae; antennal ratio in Table 2; Fl_{14} similar to Fig. 1; maxillary palpal segments 2-5 in ratio 59, 111, 148, 215μ.

Antepronotum in Fig. 21; dorsocentrals and acrostichals in Fig. 21; two-four prescutellars; humeri paler with about 10 setae; postalar area slightly paler with about 7 setae; supraalar callus dark with two setae; 12 scutellars across disc and usual fine setae anterior to these.

Leg measurements and ratios in Table 1; F I with only preapical band Ti and Ta_{1-5} I similar to Fig. 12; Ta_3 I more wholly infuscated; F II pale; Ti II apex with pale infuscation; Ta_{1-5} II missing; F III pale; Ti III as Ti II; Ta_{1-3} III pale Ta_{4-5}III appear infuscated; hairs on Ti I subequal to mesal diameter; hairs on Ti II, III about 11 x mesal diameter; claws appear simple but may be as in Fig. 18; long apical spines on Ti II missing; Ti I spur 15μ with three teeth; Ti II spur 20μ with three teeth; comb of Ti III in Fig. 17.

Wing length in Table 2; m-cu 0.31 arculus to tip; no banding present; base of Rs, r-m and m-cu as in Fig. 4; R_{2+3} appears present as in Fig. 3.

Abdominal maculation in Fig. 30; T.IX with apical band and 11 setae; Gc pale (Fig. 38); Gc measurements and HR in Table 2; megaseta of Gs (Fig. 19) 13μ L; hairs of T.VII, VIII moderately dense as in Fig. 24; darker on darker areas; apical hairs of Gc about 185μ L; anterior margin of strut 3 with a moderate spur (Fig. 38).

Holotype male.—Laguna Mozambique, 16 km SW of Puerto Lopez, Dept. del Meta, Colombia, 25-II-1972, coll. Foster.

Labrundinia hirsuta n.sp.

This is one of the most distinctive of the *Labrundinia* species here described. The pale A.I, II possibly relate it to the *L. virescens* group but the abdominal maculation (Fig. 31) with the U-shaped mark on A.VI, the mesal wing band (Fig. 40) and the dense dark hairs on A.VII, VIII (Fig. 23) will separate it from any other known *Labrundinia* species. The hairs on A.VII, VIII are very dense and in life completely hide the genitalia (Fig. 36).

Adult male.— Pedicel black with one lateral and three ventral setae; AR 1.45-1.74; Fl_{14} in Fig. 1; maxillary palpal segments 2-5 in ratio 52, 104, 144, 226μ.

Antepronotum with five-six antepronotals and two tubercles (Fig. 21); vittae very black; dorsocentrals almost join caudal acrostichals, similar to Fig. 21; about four prescutellars; humeri slightly paler; six-eight humerals; postalar area paler with nine postalars; supraalar callus dark with three setae; scutellum with nine discal setae and usual fine anterior setae (Fig. 21).

Leg measurements and ratios in Table 1; F 1 apically dark; Ti I with basal half and apex dark; Ta_1 I apex faintly dark; T_{2-5} I appear faintly infuscated; F II mesal three quarters brown; Ti II pale; Ta1 II with apical half brown; Ta_2 II with apical third brown; Ta_{3-5} II pale brown; F III brown; Ti III apical quarter brown; $Ta_{1,2}$ III apical third brown; Ta_{3-5} III pale brown; hairs on Ti I subequal to mesal diameter; hairs on Ti II, III 9-10 x mesal diameter; male claws, in ventral view unevenly bifid (Fig. 18); two pseudospurs apparently present on Ta_1 I; present on Ta_{1-4} II and on Ta_1 III; long apical spine on Ti I, 67 μ L; two long spines on Ti II, 93, 178μ; on Ti III, 137, 148μ; spur Ti I, 16μ with four teeth (Fig 11); spur Ti II with five teeth as in Fig. 7; comb Ti III with eight setae similar to Fig. 17.

Wing 1.26-1.32 mm; m-cu 0.30 arculus to tip; one wide mesal band on wing, about two thirds of wing, formed by darker hairs (Fig. 40); base of Rs, r-m, m-cu in Fig. 4; R_{2+3} present, distinct (Fig. 3).

Abdominal maculation as in Fig. 31; T.IX, arched, brown margined (Fig. 36) with about 13 setae; Gc 146-150μ L; Gc L/W 2.11-2.29; HR 1.58-1.72; Gs 85-92μ L; megaseta of Gs as in Fig. 19, 15μ L; hairs on A.I-VI pale; hairs on A.VII, VIII, dark, elongate and dense (Fig. 23); in life, almost completely shield genitalia; apical hairs of Gc pale, dense, about 266μ L; anterior margin of strut 3 with a distinct spur (Fig. 36).

Holotype male.— Laguna Mozambique, 16 km SW of Puerto Lopez, Dept. del Meta, Colombia, 25-II-1972, coll. Foster

Paratypes.— 5 males - same locality, 2 males, 6-III-1971; 3 males 9-III-1971, coll. Roback.

LITERATURE CITED

EDWARDS, F. W. 1931. Diptera of Patagonia and South Chile, Part II, Fascicle 5-Chironomidae, British Museum (Natural History): 233-331.

FITTKAU, E. J. 1962. Die Tanypodinae (Diptera: Chironomidae). Abhandlungen zur larvalsystematik der Insekten 6:453 pp.

ROBACK, S. S. 1971. The adults of the subfamily Tanypodinae (=Pelopiinae) in North America (Diptera: Chironomidae). Monographs of the Academy of Natural Sciences of Philadelphia 17: 410 pp.

ROBACK, S. S. 1987. Immature chironomids of the Eastern United States IX. Pentaneurini-Genus *Labrundinia* with the description of some Neotropical Material. Proceedings of the Academy of Natural Sciences of Philadelphia 139: this volume.

ROBACK, S. S. and N. NIESER. 1974. Aquatic Hemiptera (Heteroptera) from the Llanos of Colombia. Proceedings of the Academy of Natural Sciences of Philadelphia 126:29-49.

SAETHER, O. A. 1980. Glossary of chironomid morphology terminology (Diptera: Chironomidae) Entomologica Scandinavica Supplement No. 14: 51 pp.

Proceedings of The Academy of Natural Sciences of Philadelphia 139: 223-242, 1987

Annotated Catalog of the Type Specimens of Potts' Species of Freshwater Sponges

CECILIA VOLKMER-RIBEIRO

Museu de Ciencias Naturais, Fundação Zoobotànica do Rio Grande do Sul
Caixa Postal 1188, 90.610 Porto Alegre, RS, Brasil
and
Instituto de Biocièncias, Pontifícia Universidade Católica do
Rio Grande do Sul, Caixa Postal 1429
90.610 Porto Alegre, RS, Brasil

ANNA TRAVESET

Department of Biology, University of Pennsylvania
Philadelphia, PA, 19140

ABSTRACT.—Potts described sevemteen species of freshwater sponges, most of them from the Nearctic Region. His original descriptions contain no designation of type specimens. His collection was recently studied and we found that it contained the syntypic series for a large number of his species. For that reason holotypes by monotypy could be determined for *Heteromeyenia tubisperma* and *Ephydatia robusta*. Lectotypes and paralectotypes were selected for *Spongilla wagneri, Eunapius igloviformis, Corvospongilla novaeterrae, Radiospongilla crateriformis, Heteromeyenia repens, Heteromeyenia latitenta, Anheteromeyenia ryderi, Anheteromeyenia pictouensis, Dosilia palmeri, Trochospongilla pennsylvanica, Trochospongilla minuta,* and *Drulia rusbyi.* The Potts collection also has a fragment of the holotype of *Heteromeyenia longistylis* (Mills), topotypes of *Spongilla aspinosa, Heteromeyenia tentasperma* and *Anheteromeyenia argyrosperma* and topotypes of *Ephydatia subdivisa* (Mills) and of *Corvomeyenia everetti* (Mills). The lectotype for *Ephydatia millsii* (Mills) was selected from one specimen and one slide found in the collection. [Academy of Natural Sciences, catalog, freshwater sponges, Nearctic, Potts, types]

The majority of the presently recognized species of the Nearctic freshwater sponges were described by Potts. He did not designate holotypes or mention type deposition in his species descriptions.

Penney (1960), in a comprehensive listing of the bibliography and distribution of the freshwater sponges, presumed that the type material of Potts species was deposited in the Academy of Natural Sciences in Philadelphia.

Penney and Racek (1968) recognized fourteen out of Potts seventeen species but provided no references to syntype material except for *Dosilia palmeri* (Potts 1885) which was deposited in USNM.

As syntype material of *Trochospongilla minuta* (Potts 1887) had ben loaned to the senior author by the Academy of Natural Sciences of Philadelphia in 1973, there remained no doubt that at least part of the Potts collection was there.

The continued study of the neotropical fauna of freshwater sponges undertaken by the senior author and collaborators (Volkmer-Ribeiro 1981) made it more necessary to study the Potts' collection. Neotropical material was being collected which displayed several affinities to material described by Potts. We thus initiated contacts with Dr. George M. Davis at the Philadelphia Academy of Natural Sciences who encouraged us to study and catalog the collection.

The Potts' collection is a large one and has, in addition to his species, material of species described by other authors. The largest number of specimens were collected in the United States and Canada and are those he described in several papers or redescribed in his 1887 monograph.

The monograph contains all his species with the exception of *Spongilla wagneri* described in 1889. For that reason Potts' monograph is a paramount work to anyone working on his collection or reviewing his species.

The authors are pleased to present this paper in the centennial year of Potts' (1887) monograph.

CATALOG OF SPECIMENS

This catalog treats the specimens which Potts used to describe his seventeen species. Our main task involved the determination of holotypes by monotypy or selection of lectotypes and paralectotypes. The criteria used in that selection are discussed for each species.

We also selected lectotypes for those species of Potts placed in synonymy. The type material for each species was cataloged after the original combination but the synonymy and the present taxonomic status are also provided. Illustrations were produced whenever we considered it important; most of Potts' species are well illustrated in the 1887 monograph.

This catalog also includes a fragment of the holotype of *Heteromeyenia longistylis* Mills, topotypes of *Corvomeyenia everetti* (Mills) and of *Ephydatia millsii* (Mills). Those four species were redescribed by Potts in 1887. The 21 species thus cataloged are presently distributed in eleven genera and two families of freshwater sponges. Abbreviations used in the text: ANSP-POR, Porifera Catalog of the Academy of Natural Sciences of Philadelphia; USNM, Unites States National Museum, Washington. The original numbers by Potts follow those of the present catalog.

Most of the specimens are preserved in dried condition inside wooden boxes with Potts' numbering and handwriting on top. The collection also contains all the slides he prepared. Several of the features he illustrated can easily be observed on those slides. The labels on the slides also have Potts' handwriting. He labeled some of the specimens and slides as "type" or as "original." However, his original descriptions do not give this information.

Family SPONGILLIDAE Gray 1867

sensu Volkmer-Ribeiro, in press

Genus **Spongilla** Lamarck 1816

sensu Penney and Racek 1968

Spongilla aspinosa Potts 1880 Figs. 1 and 2

Spongilla aspinosa Potts 1880b; p. 357, no fig.
Spongilla aspinosa Potts 1887; p. 184, pl. VIII, fig. VI
Spongilla aspinosa: Penney and Racek 1968; p. 14, no fig. (and synonymy)
Spongilla aspinosa: Volkmer-Ribeiro and Maciel 1983; p. 256, no fig.

Topotypes. ANSP-PO 4525 (slide I-1); 4561 (slide I-2); 4562 (slide-3); 4560 (lot of specimens in box 2-A); E. Potts leg. October 1, 1881. Locality: Doughty's Pond, Absecum, NJ.

DESCRIPTION. The dried specimens and spicule and gemmule slides conform in every detail to Potts' (1887) description and illustrations. Slide I-1 bears a thick mounting of gemmules and sponge fragments. Box 2-A contains several dried yellow-green specimens which were encrusted on bark of logs, sphagnum, weeds, etc.; gemmules inconspicuous or absent. The microscleres of *S. aspinosa* described by Potts as smooth were however now seen under SEM analysis (Fig. 1) to bear microspines on their middle portion.

DISCUSSION. The original description of this

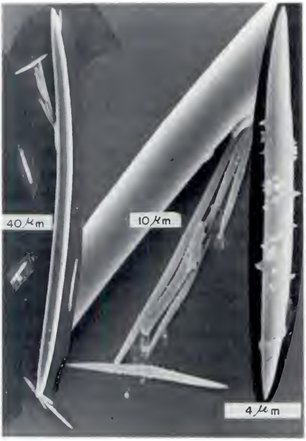


FIG. 1. *Spongilla aspinosa* Potts. SEM photograph of: Left, a megasclere and several microscleres; Middle, same at higher magnification rendering the spines on the microsclere's surface evincing the small, sparse spines on its central part. Spicular preparartions done out of a fragment of ANSP 4560.

species was evidently based upon material received prior to or during 1880. Potts states (1887, p. 185): " This sponge was first collected by Mr. R. P. Cheyney. . .during the summer of 1879 or 1880." In the original description the author only named it and provided a very short diagnosis on p. 357: "As it appeared to be entirely without spined spicules of either class." From October 1881 on Potts collected this sponge from the same area. The original specimens collected by Mr. Cheyney could not be found. The specimens and slides in the collection are dated from 1881, were collected by Potts from the type locality, and used by him to illustrate the complete description of the species he presented in his 1887 monograph.

We could not determine which of the specimens in box 2-A had gemmules without dissecting them. On slide I-1 however all of Potts' diagnostic characteristics are present, particularly the gemmules, each encased in a capsule built of megascleres (Fig. 2).

Spongilla wagneri Potts 1889 Fig. 3

Spongilla wagneri Potts 1889; p. 6, no fig.
Now: *Spongilla alba:* Poirrier 1976; p. 205. fig. 2 (and synonymy)

Lectotype. ANSP-PO 4524 (box 8), J. Willcox leg. *Paralectotypes.* ANSP-PO 4553 (slide I-15); 4554 (slide I-16); 4555 (slide I-17); 4556, 4557, 4558 (specimens in box 8-A), 4559 (specimen in box 8-B), J. Willcox leg. Locality: Creek 12 to 15 miles east of Lostman's Key, 25 miles north of Cape Sable, southwest coast of Florida, U.S.A.

DESCRIPTION. The specimen selected as lectotype is one of the largest specimens found in box 8 and has many gemmules "hidden amongst the convoluted stems of the serpulae" (Potts 1880, p. 6) upon which the sponge is encrusted. There also are numerous free gemmules inside box 8. The lectotypes and paralectotypes conform to the original description.

DISCUSSION. Potts did not illustrate *S. wagneri*. For that reason the spicules of one of the paralectotypes were analysed under SEM (Fig. 3). Poirrier (1976) placed *S. wagneri* in the synonymy of *Spongilla alba* Carter 1849, upon study particularly of the gemmoscleres. he provides a good illustration of a branching specimen of this species from Lake Pontchartrain, Lousiana.

Genus **Eunapius** Gray 1867
sensu Penney and Racek 1968

Eunapius igloviformis (Potts 1887)

Spongilla igloviformis Potts 1887; p. 202, pl. V, Fig. III; pl. VIII, Fig. V
Eunapius igloviformis: Penney and Racek 1968; p. 31, no fig. (and synonymy)

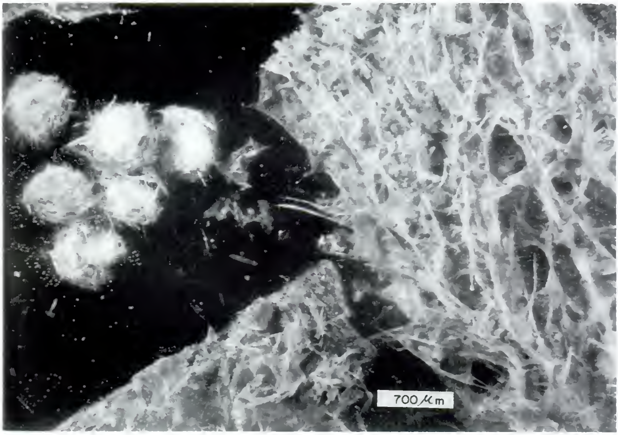


FIG. 2. *Spongilla aspinosa* Potts. Photograph of slide I-1 (ANSP 4525) showing the skeletal structure and a group of gemmules.

Lectotype. ANSP-PO 4523 (specimen in box 14A), E. Potts leg. *Paralectotypes.* ANSP-PO 4550 (slide II-1), 4551 (slide II-2), 4552 (slide II-3), E. Potts leg. Locality: Doughty's pond, Absecum, NJ.

DESCRIPTION. The lectotype is a tiny flat specimen, encrusted on a piece of log. Gemmules present, color white.

DISCUSSION. As on December 1st, 1883, date of the sponge discovery, Potts found only gemmules and on subsequent visits to the same place he: "was successful in finding and collecting growing sponges of this species ... " (1887, p. 203). The lectotype, which is a small specimen must have been collected in the first or subsequent visits since neither the specimen nor the slides bear a collecting date.

Penney and Racek (1968 p. 31) date this species from 1884 and register (p. 32) that Jewell (1959) relegated *S. igloviformis* to synonymy of *S. mackayi* Carter 1885 "without giving any reasons for her decision. " In his 1884 paper Potts refers to an *S. iglooiformis* received from Mr. Mackay from a lake near Pictou, Nova Scotia, but neither offers a description nor declares it a new species. However, in 1887, he describes *S. igloviformis* as a new species and makes no reference, as he usually does, to a prior work. So the correct year for *S. igloviformis* is 1887 and *S. iglooiformis* is declared a "nomen nudum." Potts also states, 1887, p. 204: "From Mackay's Lake, near Pictou, Nova Scotia, Mr. A. H. Mackay has kindly sent what seems to me the same or a nearly related species, which was described a year later by Mr. Carter under the name of *S. mackayi*."

Corvospongilla Annandale 1911
sensu Penney and Racek 1968

Corvospongilla novaeterrae (Potts 1886) fig. 4
Spongilla novaeterrae Potts 1886; p. 227, fig. 1

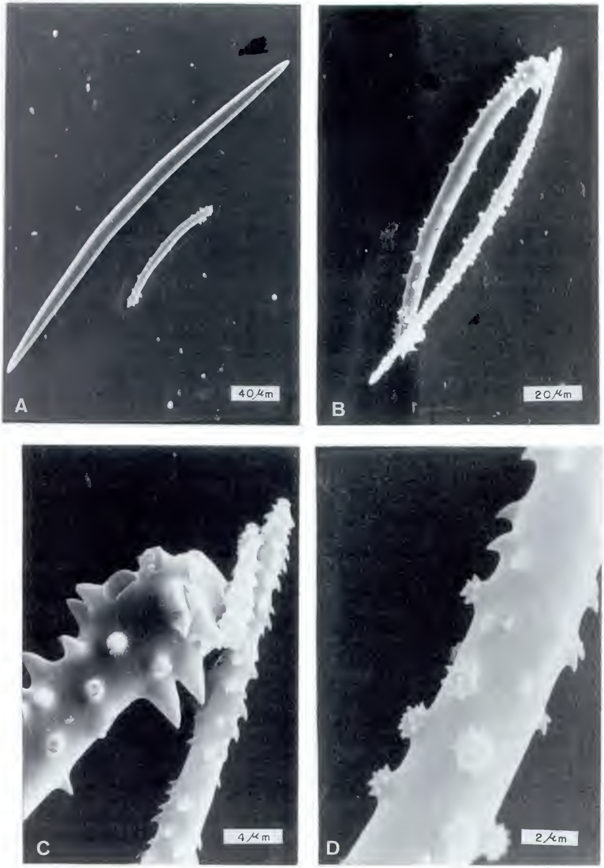


FIG. 3. *Spongilla wagneri* Potts. SEM analysis of the spicular components of the paralectotype ANSP 4559. **A**, megasclere and gemmosclere at low magnification. **B**, gemmosclere and microsclere at higher magnification. **C**, detail of the extremities of gemmosclere and microsclere seen in B. **D**, abrupt transition of the spines found at the extremities of the microscleres to the microspined protuberances found at their central part.

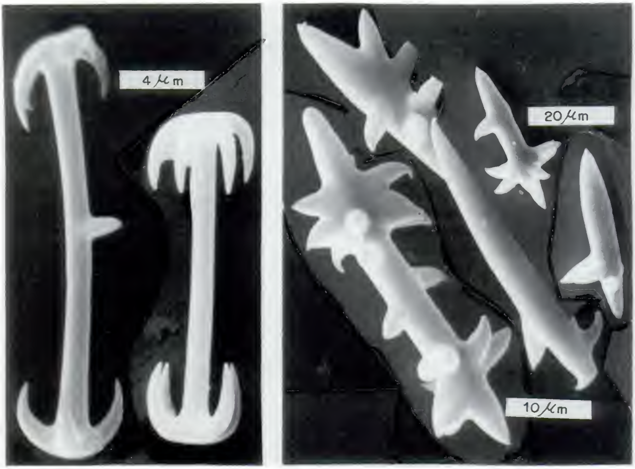


FIG. 4. *Corvospongilla novaeterrae* (Potts): SEM photograph of the spicular components of the paralectotype ANSP 4545. Left, two microscleres. Right, several gemmoscleres.

Spongilla novaeterrae Potts 188; p. 206, fig. 1
Corvospongilla novaeterrae: Jewell 1952; p. 454, no fig.

Lectotype. ANSP-PO 4521 (specimen in box 15-B), A. H. Mackay leg. August, 1885. *Paralectotypes.* ANSP-PO 4522 (largest stone with encrusted sponge, box 15-B), 4543 (slide II-5), 4544 (slide II-6), 4545 to 4549 (five specimens encrusted on small stones, box 15-A), A. H. Mackay leg. August 1885. Locality: Lakes or ponds at the vicinity of Heart's Content, Avalon Peninsula, Newfoundland, Canada.

DESCRIPTION. The lectotype was selected from a syntypic series of two slides plus 7 specimens encrusting on small stones. The lectotype is a small specimen which bears several conspicuous gemmules and displays all the features described by Potts. The paralectotypes are minute or mingled with algal growths and with a few gemmules or devoid of them.

DISCUSSION. Potts (1887) did not report other findings or collections of this sponge. Therefore, the material of *C. novaeterrae* in the collection is syntypic. Penney and Racek (1968) examined the e type slides and proposed that *S. novaeterrae* be not considered a distinct species but product of sexual hybridization between *Corvomeyenia everetti* Mills and a species of "some other genus" (p. 124), because of "the presence of unmistakably typical microbirotulates of *C. everetti* in the spicular mixture of *S. novaeterrae* and the grossly malformed gemmoscleres." However, the present study of those same slides (Fig. 4) revealed that not only are the microscleres different in size and shape in the two involved species, but also there are differences in the megascleres, the gemmoscleres, the skeletal structure, the gemmular coating and the gemmule position in the skeleton. Such differences are well documented in the original description of *S. novaeterrae* and in the Potts 1887 redescription of the two species. We thus reinforce here Jewell's 1952 correct assignment of *S. novaeterrae* to the genus *Corvospongilla*.

Genus **Radiospongilla**
Penney and Racek 1968

Radiospongilla crateriformis (Potts 1882)

Meyenia crateriformis Potts 1882; p. 12, no fig.
Meyenia crateriformis Potts 1887; p.228, pl. V. Fig. VI, pl. X, fig. v.
Radiospongilla crateriformis: Penney and Racek 1968; p.66, pl. 5, figs. 1-3, pl. 6, figs. 1,2. (and synonymy)

Lectotype. ANSP-PO 4529 (larger specimen in box 27-A), E. Potts leg. September 1881; *Paralectotypes*. ANSP-PO 4567 (smaller specimen in box 27-A), 4568 (slide III-1), 4569 (slide III-2), 4570 (slide III-3) E. Potts leg. September 1881. Locality: Crowe's Mill, Brandywine Creek near Chadd's Ford, PA.

DESCRIPTION. Both specimens small, the lectotype selected is the largest one, gemmuliferous, light yellowish green, texture very loose. Specimens and slides conforming to Potts' original and his 1887 enlarged description.

DISCUSSION. Potts (1887 p. .229) reports only one collecting trip to the Brandywine Creek, and that is the only material of *R. crateriformis* from this site in his collection. Therefore, those specimens are syntypes.

Genus **Ephydatia** Lammouroux 1816
sensu Penney and Racek 1968

Ephydatia millsii (Mills 1884)

Meyenia millsii Mills 1884; p. 147, no fig.
Meyenia millsii : Potts 1887; p. 225, pl. X, fig. II
Meyenia millsii: Kellicot 1891; p. 103, no fig.
Ephydatia millsii: Penney and Racek 1968; p. 95, pl. 7, figs. 1-3, (and synonymy)

Lectotype. ANSP-PO 4527 (specimen in box 25 and slide II-26), H. Mills leg. March 17, 1884. Locality: Sherwood Lake, near Deland, FL.

DESCRIPTION. Very small, whitish sample. Gemmules present. The specimen and the spicules in slide II-26 conform to the original description.

DISCUSSION. The original description of this species by Mills (1884) offers no indication of the presence of more than one specimen. The same is also true for Potts' description which appeared in 1887.

However, Kellicot (1891, p. 103) records the existence of "many small pieces of this sponge collected by Mr. Mills in Sherwood Pond, Deland, Fla. , March 1884." Mills 1884, p. 147 writes: "This sponge was sent from Florida to Mr. Potts for him to describe and name if he chose. He considered it quite new and named it as above, without description." From this reading one may assume that Potts sent the specimen back to Mills and kept a small piece for his collection. Since we did not succeed in getting information on the present location of the Mills collection, and to avoid assumption of a holotype by monotypy, we prefer to consider the material in Philadelphia lectotype, implying that slide II-26 was made from the small piece in box 25.

Penney and Racek (1968) followed the general assumption that Potts 1887 was the author of the species. However Mills 1884 was the first to publish the name, description, and statement about the species novelty. According so to article 12 of the 1985 International Code of Zoological Nomenclature, Mills and not Potts must be considered the author of the species.

Ephydatia subdivisa (Mills 1884)

Meyenia subdivisa Mills 1884; p. 147, no fig.
Meyenia subdivisa: Potts 1887; p. 226, pl. IX, fig. VI
Now: *Ephydatia fluviatilis*: Poirrier 1974: p. 338, no fig. (and synonymy)

Topotypes. ANSP-PO 4528 (in box 26-A), 4571 (slide II-27), 4572 (slide II-28), H. Mills leg. March, 1884. Locality: St. John's River, near Palatka, FL.

DESCRIPTION. Specimen encrusted on a piece of log, color yellow-green, gemmules present. Spicules in the slides conforming to Potts illustration.

DISCUSSION. The authorship of this species must be also credited to Mills (1884) and not to Potts (1887) as referred by Penney and Racek (1968). Their statement that Mills (1884) presented no description of the species is incorrect. Penney (1960) already recognized Mills (1884) as the author of this species. Departing from this fact the material of *M. subdivisa* found in the Potts collection was cataloged as topotype since the lectotype should be selected from specimens in the Mills collection. Mills states that the sponge was abundant on piles of the dock at Palatka and other parts of the St. John's River so the probability is that the description of this species was based upon specimens from different sites. Potts also states: "the finest specimen of *M. subdivisa* grew upon the bark of a submerged pine log." (p. 277), so even Potts saw more than one specimen when preparing the redescription of the species. For that reason the slides in his collection received each a number, presumably prepared from different specimens. Kellicot (1891) does not list material of this species in his study of the Mills collection.

Ephydatia robusta (Potts 1887)

Meyenia robusta Potts 1887; p.225, pl. IX, fig. V
Ephydatia robusta: Penney and Racek 1968; p. 91, pl. 7, figs 11,12
Now: *Ephydatia fluviatilis*: Poirrier 1974; p. 338, fig. 3 (and synonymy)

Holotype. ANSP-PO 4526 (specimen in box 24 and slide II-25), Dr. Geo. H. Horn leg., no date. Locality: Honey Lake Valley, near Susanville, CA.

DESCRIPTION. Sponge massive, encrusting. Yellow color. Sample not so big as stated by Potts. Gemmules present. Spicules in slide II-25 conforming to the original description and illustration.

DISCUSSION. This species was certainly based upon the sole specimen found by Potts in the Academy of Natural Sciences since that is the only material that Potts refers to in the original description. He was indeed very careful in registering the origin of the specimens and the general distribution of the sponges being described. This discrepancy between the reported large original specimen and the small sample presently found must be due to further fractioning of the specimen.

Genus **Heteromeyenia** Potts 1881
sensu Penney and Racek 1968

Heteromeyenia tentasperma (Potts 1880)

Spongilla tentasperma Potts 1880a; p. 330, no fig.
Spongilla tenosperma: Potts 1880b; p. 357, no fig.
Carterella tenosperma Potts 1881a; p. 150, no fig.
Carterius tenosperma Potts 1887; p. 265, pl. VI, fig. VI, pl. XII, fig. IV
Heteromeyenia tentasperma: Penney and Racek 1968; p. 112, pl. 9, figs 8, 9, 18 (and synonymy)

Topotype. ANSP-PO 4533 (specimen in box 42-A and slides IV-26, 27, 28), E. Potts leg., 1882. Locality: Landsdowne Run, Centennial Grounds, Fairmount Park, Philadelphia, PA.

DESCRIPTION. Sponge small, yellowish green, gemmules present. The specimen and the slide conform to the original description and the 1887 redescription. The peculiarity of the foraminal appendages could be confirmed in the slide mountings.

Discussion. Only the material (specimen and slides) dated from 1882 was found in the collection. Since Potts described the species in 1880 the specimen and the slides now cataloged do not belong to syntypic series. Potts in fact reports (1887) the collecting of this sponge in the same place in the years after 1880.

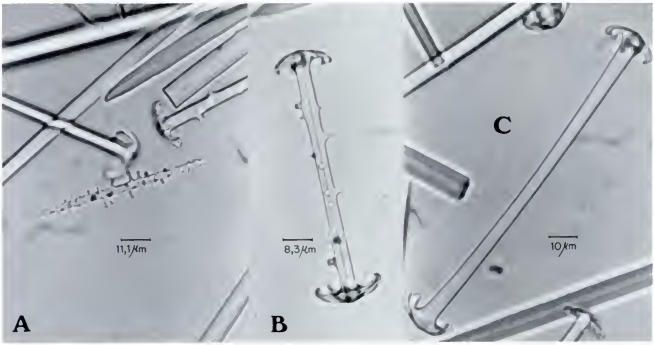


FIG. 5. *Heteromeyenia longistylis* Mills. Light Microscope photograph of spicules of holotype ANSP 4539. A, Details of microsclere, rotules of one long and one short gemmoscleres and of sparsely spined megascleres. B, Short, spined gemmosclere. C, Long, smooth gemmosclere.

Heteromeyenia repens (Potts 1880)

Spongilla repens Potts 1880 b; p.357, no fig.
Heteromeyenia repens Potts 1881 a p. 150, no fig.
Heteromeyenia repens Potts 1887; p. 237, pl. XI, fig III
Now: *Heteromeyenia baileyi*: Penney and Racek 1968; pl. 9, figs.1-4, 15 (and synonymy)

Lectotype: ANSP-PO 4535 (specimen on the smaller fragment of log in box 30-A), E. Potts leg. October 13, 1880. *Paralectotypes*. ANSP-PO 4579 (specimen on the largest fragment of log in box 30-A), 4580 (slide III-11), 4581 (slide III-12), 4582 (slide III-13), E. Potts leg., October 13, 1880. LOCALITY: Lehigh River at Lehigh Gap, PA.

DESCRIPTION. Dry sponge yellowish green, thin encrusting on two fragments of log, bearing many gemmules. Lectotype and paralectotypes displaying the features Potts described in his 1887 lengthened study of this species.

DISCUSSION. Since Potts (1887, p. 238.) reports the collecting of this species only once (October 13, 1880) from that locality and the specimens and the slides bear this date there is no doubt that the upper listed material pertains to the syntypic series. Penney and Racek 1968 placed *H. repens* in the synonymy of *H. baileyi*, described by Bowerbank 1863 upon material received from "a stream on the Canterbury Road, near West Point, New York" (Potts 1887, p. 239). Those authors recognized in the type material of *H. baileyi* the short class of birotulate gemmoscleres described by Potts for *H. repens* and omitted by Bowerbank in the description of *H. baileyi*.

Heteromeyenia tubisperma (Potts 1881)

Carterella tubisperma Potts 1881a; p. 150, no fig.
Carterius tubisperma Potts 1887; p. 263, pl. VI, fig. III
Carterius tubisperma: Kellicot 1891; p. 104, no fig.
Heteromeyeenia tubisperma: Penney and Racek 1968; p. 113, pl. 9, figs. 5-7, 17 (and synonymy)

Holotype. ANSP-PO 4532 (two fragments in box 40), 4573 (slide IV-19), 4574 (slide IV-20), 4575 (slide IV-21). Dr. David Kellicot leg. October 11, 1870. Locality: Niagara River, Buffalo, NY.

DESCRIPTION. Two small fragments of a sponge of green color with many large gemmules present. The fragments and the gemmules and spicules in the slides conform to the original description and Potts' 1887 redescription. Slide IV-20 has the first label concealed under Potts' label.

DISCUSSION. Penney and Racek (1968) correctly assigned the species authorship to Potts in spite of the fact that Mills 1880 was the first to produce a detailed description of the specimen. However he failed to declare and nominate it a new species which was done by Potts in his 1881 description. The holotype by monotypy can be easily determined by Mills 1880 statement (p. 132): "The other specimen found by Prof. Kellicot and presented to me by him is, I think, a new species." The two fragments (and probably also slide IV-20) sent to Potts as well as the slides prepared by Potts himself, all are from the type locality. Kellicot 1891, p. 104, registered in his notebook "the day of the find. . . October 11, 1879," but makes no reference to this particular specimen in his study of the Mills collection. We conclude that Mills sent to Potts all the material used in his 1880 description.

Heteromeyenia latitenta (Potts 1881)

Carterella latitenta Potts 1881 b; p. 176, no fig.
Carterius latitenta Potts 1887; p. 264, pl. VI, fig. V, pl. XII, fig. V
Heteromeyenia latitenta Penney and Racek 1968; p. 111, no fig. (and synonymy)

Lectotype. ANSP-PO 4534 (fragments in box 41-A), E. Potts leg. July 1881. *Paralectotypes*. ANSP-PO 4576 (slide IV-22), 4577 (slide IV-23), 4578 (slide IV-24), E. Potts leg., July 1881. Locality: Chester Creek, Chester County, PA.

DESCRIPTION. Many small pieces and a large one encrusting the inner side of a bivalve shell, also many gemmules present. The features observed on the slides, particularly the foraminal structure of the gemmules, entirely conform to Potts original and his 1887 redescription and illustration for this species.

DISCUSSION. In spite of the fact that Potts recorded in his 1887 paper that the sponge was abundant when he first discovered it at Chester Creek, the actual collections were rather poor. No other material of this species from Chester Creek was found in his collection.

Heteromeyenia longistylis Mills, 1884 Fig. 5

Heteromeyenia longistylis Mills 1884; p. 146, no fig.
Heteromeyenia longistylis Potts 1887; p. 242, no fig.
Heteromeyenia longistylis: Penney and Racek 1968; p. 105, no fig.

Holotype: ANSP-PO 4539 (slide III-18) from fragment of holotype). Dr. Wolle leg. No date. Locality: Lehigh River, Bethlehem, PA.

DESCRIPTION. The slide contains the spicular categories (Fig. 5) including the microscleres referred to by Potts (1887) and shows his redescription to be an acurate one. This slide differs a little from the ones prepared by Potts and one can see an original label concealed under Potts label.

DISCUSSION. Mills (1884) when describing this species stated at p. 146: "Specimen very small and few statoblasts." Potts on the other hand writes (p. 242) that he had a "very minute fragment" of this sponge upon which he had prepared a description several years prior to his 1887 redescription. The holotype by monotypy is thus clearly established. Since no fragment could be found in the Potts collection, the slide is the only remnant in his collection of the sole specimen upon which Mills described the species and represents a part of that specimen. However doubt remains whether it was prepared out of that minute fragment received by Potts or whether it is one of the original Mills slides. This species was never illustrated before.

Mills did not refer to the locality in his original description and Potts seemed uncertain of its coming from the Lehigh River since the question mark after the word Philadelphia is his. We believe that Potts inferred the locality from his knowledge of the area where Dr. Wolle used to collect. (Potts 1884, p. 216). Kellicot (1891) makes no reference to material of this species in the Mills collection.

Genus **Anheteromeyenia** Schröder 1927
sensu Penney and Racek 1968

Anheteromeyenia argyrosperma (Potts 1880) Fig. 6

Spongilla argyrosperma Potts 1880 b; p. 357, no fig.
Heteromeyenia argyrosperma Potts 1881 a; p. 150, no fig.
Heteromeyenia argyrosperma Potts 1884; p. 239, no fig.
Heteromeyenia argyrosperma Potts 1887; p. 239, pl. VI, fig. I
Anheteromeyenia argyrosperma: Penney and Racek 1968; p. 116, pl. X figs. 8-10 (and synonymy)

Topotypes. ANSP-PO 4538 (specimen in small box A inside box 31 labelled as "original"), 4587 (other pieces in box 31), 4588 (slide III-14), 4589 (slide III-15), 4590 (slide III-16), E. Potts leg. November 14, 1881. Locality: Lehigh River at Lehigh Gap, PA.

DESCRIPTION: Small sample, sponges minute and of gray color and loose texture encrusting on fragments of burned wood.

DISCUSSION. No specimen or specimens were found dated from 1880 or prior to that year. So the material labeled by Potts as "original" does not belong to the syntypic series unless the author placed what would be the holotype, with no date, inside the box containing the specimens collected on Nov. 14, 1881. As that would be an "assumption of holotype" to be avoided according to the Recommendation 73F of the International Code (1985) the present authors prefer not to elect lectotypes and paralectotypes and consider the above listed specimens as topotypes.

Anheteromeyenia ryderi (Potts 1882) Fig. 7.

Heteromeyenia ryderi Potts 1882; p. 13, no fig.
Heteromeyenia ryderi Potts 1884; p. 216, no fig.
Heteromeyesdnia ryderi Potts 1887; p. 242, pl .XI, figs. IV, V, and VI.
Anheteromeyenia ryderi:: Penney and Racek 1968; p. 117, pl. 10, figs. 1-4. (and synonymy)

Lectotype. ANSP-PO 4536 (largest specimen in box 32-A), E. Potts leg. 1881. *Paralectotypes.* ANSP-PO 4583 (6 smaller pieces in box 32-A), 4584 (slide III-19), 4585 (slide III-20), 4586 (slide III-21), E. Potts leg. 1881. Locality: Indian Run, a branch of Cobb's Creek, whose waters at the time reached the Delaware River below Philadelphia.

DESCRIPTION. Dry sponge greenish yellow, texture loose, many gemmules present at the basal part of the sponge.

DISCUSSION. There is no collecting date in the box or on the slide labels. Box 32 bears an indication of "type " in Potts' handwriting. Also in legend of plate XI the author (1887, p. 278) states that to be an illustration of the type. However in the original description there was no corresponding statement and in box 32 there were seven pieces of sponge from Indian Run. Potts states at p. 243 that he collected this species from Indian Run only once. The specimens in the collection from that location are thus syntypes from which a lectotype and paralectotypes could be selected.

Anheteromeyenia pictouensis (Potts) Fig. 8

Heteromeyenia pictouensis Potts 1885a; p. 28, figs. A,B,C.
Heteromeyenia pictovensis Potts 1886; p. 228, no fig.
Heteromeyenia ryderi var. *pictovensis* Potts 1887; p. 244, pl. XI, fig. VI
Anheteromeyenia pictovensis: Penney and Racek 1968; p. 119, pl. 10, figs. 5-7 (and synonymy)

Lectotype. ANSP-PO 4537 (slide III-23), A. H. Mackay leg. December, 1884. *Paralectotypes*: ANSP-PO 4565 (slide III-23), 4566 (specimens inside three envelopes in box 32 N), A. H. Mackay leg. 1884. Locality: Several lakes upon the watershed of Pictou, Nova Scotia.

DESCRIPTION. Slide III-23 bears all the spicules (gemmoscleres and megascleres) illustrated

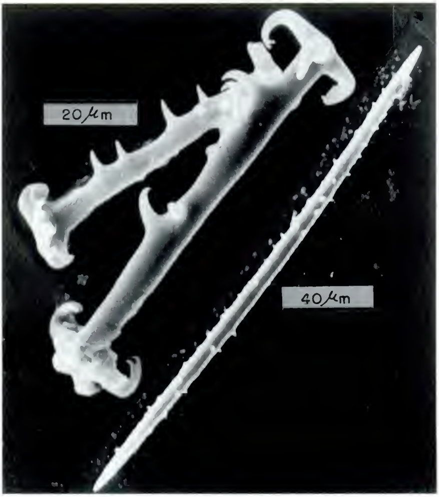


FIG. 6. *Anheteromeyenia argyrosperma* (Potts). Top, The two classes of gemmoscleres at high magnification. Bottom, Photo of one megasclere at low magnification. Spicular preparations from the topotype ANSP 4587.

in Potts' original description and his 1887 paper. However on both slides (III-22 and III-23) a third kind of spicule (Fig. 8) was abundant which looks like the microscleres of genus *Spongilla* . The specimens in box 31-N are small fragments without gemmules.

DISCUSSION. The slide collection houses only two slides of *A. pictouensis* . Because slide III-23 has many gemmoscleres, it was selected as the lectotype. Potts remarked in the original description that the first specimens, discovered by Mr. Mackay during the summer of 1884, had no gemmules and that only the second ones collected on "the last week of December" [p. 29] "were seen, after an exhaustive search to bear a few, and but a few gemmules." This way it was possible to assign the two slides with gemmoscleres to that second collecting trip. How does one explain the presence of a third kind of spicule which looks like microscleres? Remember that Potts states: "Dermal spicules absent or undiscovered" (p. 28). We advance the hypothesis that this kind of spicule could be a contamination from other species in the area since Potts (1884, p. 216) reports the finding there of several other species for instance *Spongilla lacustris*. In the original description the name of the species is printed as "*pictouensis*" because the author followed a suggestion by Mr. Mackay to nominate the new species after the specific locality. What looks like a misprinting first appeared in Potts' 1886 paper and from then on one or the other printing were used as can be seen in the synonymy presented by Penney and Racek 1968. The original name is now restored.

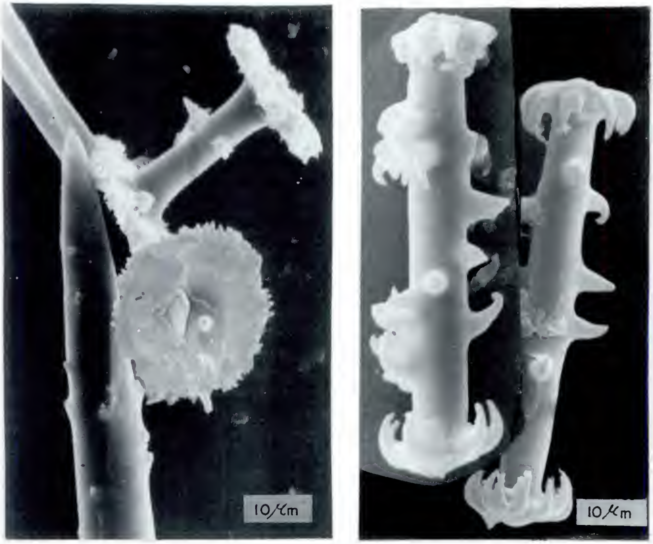


FIG. 7. *Anheteromeynia ryderi* (Potts). SEM photos of the spicules found in the lectotype. Left, two gemmoscleres of the shorter class and the extremity of a megasclere. Right, two gemmoscleres of the longer class

Genus **Dosilia** Gray 1867
sensu Penney and Racek 1968

Dosilia palmeri (Potts 1885) Fig. 9

Meyenia plumosa var. *palmeri* Potts 1885b; p. 587, pl. VI, figs. a-g.
Meyenia plumosa var. *palmeri* Potts 1887, p. 234, pl. X, fig. VI.
Dosilia palmeri: Penney and Racek 1968 , pl. II, figs. 6-9 (and synonymy)

Lectotype. USNM 5419 E. Palmer leg. May 21, 1885. *Paralectotypes*. USNM 34054, 34055, 34056, 34057 (each one a fragmented specimen), ANSP-PO 4531 (slide III-7), ANSP-PO 4563 (several small fragments and numerous gemmules). E. Palmer leg. May 21, 1885. Locality: Banks of the Colorado River near Lerdo, Sonora, Mexico.

DESCRIPTION. The extreme fragility of this sponge, a character remarked by Potts, certainly accounts for the fact that none of the five specimens deposited in the USNM is in what must have been its original sub-spherical shape. Since the largest specimen was the least fragmented one it was selected as lectotype. Only that specimen (Fig. 9A) displays what seems to have been an oscular area. However that orifice could also have resulted from the loss of a central fragment.

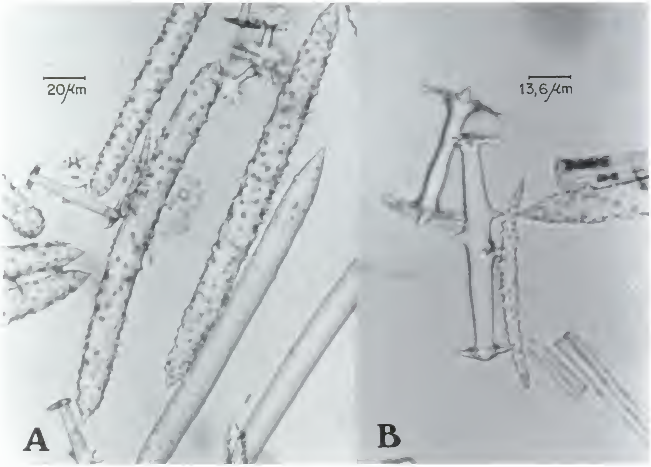


FIG. 8. *Anheteromeynia pictouensis* (Potts). Light microscope photographs of spicules of lectotype ANSP 4537. **A**, the megascleres and the two classes of gemmoscleres are shown. **B**, one short class and one long class gemmosclere are shown at high magnification. Both photographs reveal the presence of microscleres not reported by Potts .

The observations of figs. 9A and B evince that Dr. Palmer collected the specimens by sectioning the screw bean twigs which supported them. The spicules on slide III-7 conform to Potts' original illustrations.

DISCUSSION. Potts (1887, p. 236) reports the study of five "sponge masses" and five specimens deposited in USNM which were collected by Dr. Palmer on May 21, 1885 from the Colorado River near Lerdo; these specimens are syntypes. The fragments and slide which remained in the Academy at Philadelphia must be part of one or another of those five specimens and obviously are part of the syntypic series. The spicular category compared by Potts to "a hedgehog or Scotch terrier" (1885, p. 587) though not illustrated in the present catalog were detected again in slide III-7 and in spicular preparations presently done out of the lectotype and the paralectotypes.

Genus **Trochospongilla** Vejdovsky 1883
sensu Penney and Racek 1968

Trochospongilla pennsylvanica (Potts 1883)

Tubella pennsylvanica Potts 1882; p. 14, no fig.
Tubella pennsylvanica Potts 1887; p. 251, pl. VI, fig. II, pl. XII, figs. I, II, III.
Trochospongilla pennsylvanica: Penney and Racek 1968 ; p. 137, pl. 12, figs. 3, 4 (and synonymy)
Trochospongilla pennsylvanica: Volkmer-Ribeiro and Maciel 1983; p. 257, fig. 6
Trochospongilla pennsylvanica: Volkmer-Ribeiro and De Rosa-Barbosa 1985; p. 84, fig. 14

Lectotype. ANSP-PO 4540 (slide IV-4), E.

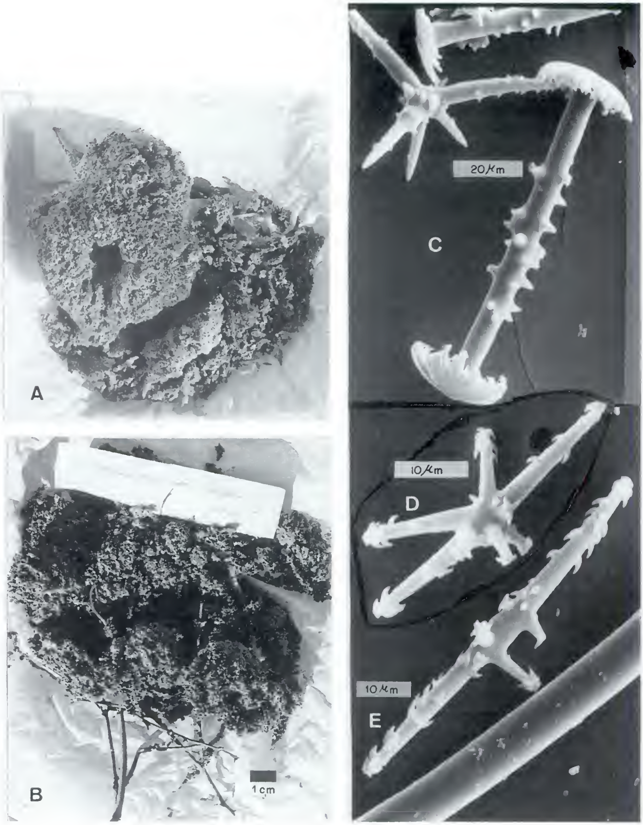


FIG. 9. *Dosilia palmeri* (Potts). **A**, frontal view of the holotype with oscular (?) area. **B**, paralectotype (USNM 34055) evincing the sponge extreme fragility. **C**, SEM of microsclere and gemmoscleres. **D**, SEM of another microsclere. **E**, SEM of yet another microsclere and detail of the spine covering on the central part of the megascleres. The SEM photos were made upon spicular preparations from the lectotype.

Potts leg. November, 1881. *Paralectotypes.* ANSP-PO 4564 (slide IV-5), E. Potts leg. November, 1881. Locality: Lehigh River at Lehigh Gap, PA.

DISCUSSION. The only material of the syntypic series of *T. pennsylvanica* in the Potts collection are two slides, dated from November, 1881 from the type locality. Potts (1887 p. 251) reported the first specimens he found to be minute and with a poorly developed skeleton. He may have used those first specimens in the preparation of the two slides.

Trochospongilla minuta (Potts 1887)

Meyenia minuta Potts 1887; p. 218, no fig.
Trochospongilla minuta: Volkmer-Ribeiro 1973; p. 137, pl. 1, figs. 1-4
Trochospongilla minuta: Volkmer-Ribeiro 1976; p. 274, figs. 1, 2
Trochospongilla minuta: Volkmer-Ribeiro and De Rosa-Barbosa 1985; p. 84, figs. 6, 10, 25, 26.

Lectotype. Slides II-18 and II-19, Dr. H. H. Rusby leg. no date. *Paralectotypes*. ANSP-PO 4530 (specimens in box 38-C-4), Dr. H. H. Rusby leg., no date. Loclaity: Small branch of the river Beni in Eastern Bolivia, South America.

DESCRIPTION. The spicules and gemmules in slides II-18 and II-19 were illustrated in the redescriptrion of this species by Volkmer-Ribeiro (1973). The specimens elected as paralectotypes are two minute specimens encrusted on a leaf belonging to the stem upon which a mass of the sponge *Drulia browni* (Bowerbank 1863) had formed.

DISCUSSION. Slides II-18 and II-19 have a same catalog number because the authors considered them as prepared from the same minute specimen. Potts stated (1887, p. 219) "The first was found accidentally on a mount containing another sponge and a very careful and almost despairing search was required before another was discovered." Looking on the several leaves fallen from the branch containing the *Drulia browni* specimen, we could detect the one containting the other two specimens. Because they are minute and grew close together on the same leaf, they are given the same catalog number. The minuteness of this sponge is well illustrated in Volkmer-Ribeiro 1976 figs. 1 and 2. Slides II-18 and II-19 were wrongly quoted by Volkmer-Ribeiro (1973) as holotype.

After the preparation of the redescription of *T. minuta* in 1973 the senior author returned the two slides to the Academy. They were acknowledged as returned by Mr. Samuel Fuller, curator of the collection at that time. However slides II-18 and II-19 could not be located at the time of the present study and for that reason could not receive a number as lectotype.

Family METANIIDAE
Volkmer-Ribeiro 1986

Genus Corvomeyenia Weltner 1913

Corvomeyenia everetti (Mills 1884) Figs. 10-11

Meyenia everetti Mills 1884; p. 146, no fig.
Meyenia everetti: Potts 1884; p. 216, no fig.
Meyenia everetti: Potts 1887; p. 230, pl. X, figs III and IV.
Meyenia everetti: Kellicot 1891; p. 103, no fig.
Corvomeyenia everetti: Harrison 1971; p. 132, figs. 4, 5, 6 (and synonymy)
Corvomeyenia everetti: Volkmer-Ribeiro 1986; p. 502, fig. 4.

Topotype. ANSP-PO 4594 (specimen in flask in box 50), 4542 (slide III-5), 4593 (slide III-4), E. Potts leg. September 23, 1886. Locality: Gilder Pond, Mt. Everett, Berkshire Co., MA.

DESCRIPTION. The specimen no. 4594 was originally preserved in alcohol but is now dried and pasted against the flask walls. The specimen and the slides conform to all details in Potts 1887 redescription of this species. Slide III-5 was carefully prepared and eosin stained by Potts and perfectly illustrates the fragile, branched structure of this sponge and the particular distribution of its gemmules "found axially, in a single series along the fronds, each enclosed in a rather loosely

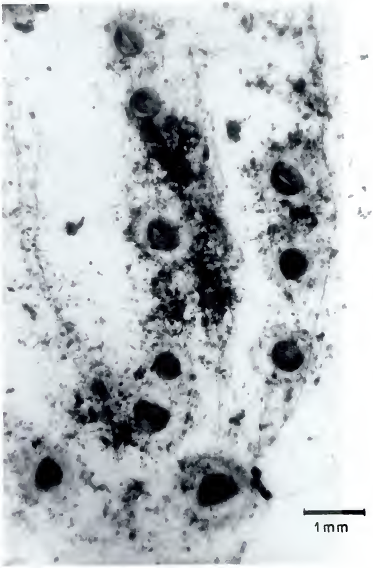


FIG. 10. *Corvomeyenia everetti* (Mills). Photograph of slide III-5, ANSP 4542, illustrating the branching, extremely fragile structure of the skeleton and the encapsulated gemmules axialy distributed along the fronds.

formed capsule or cage of skeleton spicules, the diameter of which is much greater than that of the included gemmule" (Potts 1887, p. 230/31, Fig. 10).

DISCUSSION. Kellicot reports (1891 p. 99) being in charge of preparing a representative set of specimens of the Mills collection for the Buffalo Society of Natural Sciences. Since he registers the existeence in that collection of "specimens" of the syntypic series, a lectotype must be selected from that series. The authors did not succeed, however, in gathering information on the present location of the Mills colection.

Genus **Drulia** Gray 1867
sensu Mothes de Moraes 1983

Drulia rusbyi (Potts 1887)

Parmula rusbyi Potts 1887; p. 259, no fig.
Now: *Drulia browni*: Mothes de Moraes 1983; p. 16, figs. 105, 18-21 (and synonymy).

Lectotype. ANSP-PO 4541 (slide IV-17), Dr. H. H. Rusby leg., no date. *Paralectotypes*. ANSP-PO 4591 (specimen in box 38-C), 4592 (slide IV-18), Dr. H.H. Rusby leg., no date.

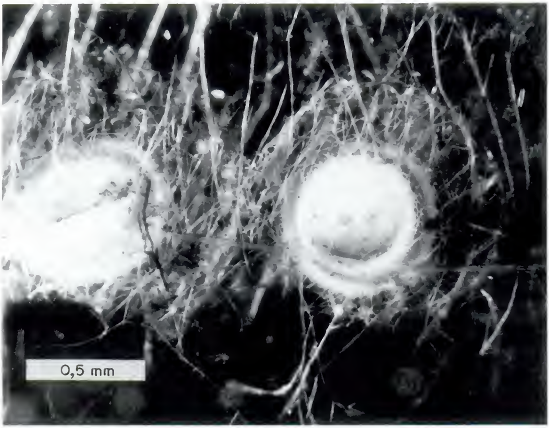


FIG. 11. *Corvomeynia everetti* (Mills). Detail of the gemmular capsule seen in Fig. 10. The capsular walls are seen to be formed of megascleres.

Locality: Beni River, Bolivia, South America.

DESCRIPTION. The specimen and the slides conform to the original description.

DISCUSSION. The label of slide IV-17 bears the word "Type." However because there was no formal designation of type in the original description a lectotype was elected. Also the original description indicates the existence of more than one specimen as confirmed by study of the collection. The present study of this syntypic series confirmed Mothes de Moraes' assumption that this species should be placed in the synonymy of *Drulia browni* (Bowerbank 1863).

ACKNOWLEDGMENTS

We are indebted to Dr. George M. Davis, for his deep interest on the problem and for all the facilities made accessible during our work. We are grateful to Dr. Arthur E. Bogan for help with finding specimens, interpreting data and discussion of the process of type cataloging. We also thank Mary McKee for her help with photographs for figures 5 and 8. The senior author acknowledges the cooperation of Dr. Klaus Ruetzler, Smithsonian Institution with loan of syntype material of *Dosilia palmeri*; she is grateful to Dr. Francisco Kees, from Faculdade de Engenharia of Universidade Federal do Rio Grande do Sul for the SEM photos and to Dr. Arno A. Lise for the photos of lectotype and paralectotype of *Dosilia palmeri* ; she acknowledges the granting of fellowship no. 30.6134/76 of Conselho Nacional de Desenvolvimento Cientifico e Tecnológico (CNPq) Brazil as well as funds granted to her by the same CNPq. (Grant no. 4058993/85) which made possible her visit to Philadelphia.

LITERATURE CITED

ANNANDALE, N. 1911. Freshwater sponges, hydroids and Polyzoa. Pages 1-126, 241-245 *in* The fauna of British India, including Ceylon and Burma. Taylor and Francis, London.

ANNANDALE, N. 1918. Zoological results of a tour in the Far East. II Freshwater Sponges from Japan, China and the Malay Peninsula. Memoirs of the Asiatic Society of Bengal 6: 199-216.

Bowerbank, J. S. 1863. A monograph of the Spongillidae. Proceedings of the Zoological Society of London 1863: 440-472.

Gray, J. E. 1867. Notes on the arrangement of sponges, with the description of some new genera. Proceedings of the Zoological Society of London 1867: 492-558.

Harrison, F. W. 1971. A taxonomical investigation of the genus *Corvomeyenia Weltner* (Spongillidae) an with an introduction of *Corvomeyenia carolinensis* sp. nov. Hydrobiology 38 (1): 123-140.

International Code of Zoological Nomenclature 1985. 3rd ed. London, International Trust for Zoological Nomenclature, 1985: 337 pp.

Jewell, M. E. 1952. The genera of North American freshwater sponges, *Parameyenia,* new genus. Transactions of the Kansas Academy of Sciences 55 (4): 445-457.

Kellicot, D. S. 1891. The Mills collection of freshwater sponges. Bulletin of the Buffalo Society of Natural Sciences 5: 99-104.

Mills, H. 1880. Freshwater sponges. The American Journal of Microscopy 5 (6): 125-132.

Mills, H. 1884. Thoughts on the Spongidae, with reference to the American sponges of the fresh water group with some accounts of them in detail. Proceedings of the American Society of Microscopists 1884: 131-147.

Mothes de Morales, B. 1983. Revisão do genero *Drulia* Gray 1867 (Porifera-Spongillidae). Iheringia, série Zoologia 62: 13-36.

Penney, J. T. 1960. Distribution and bibliography (1892-1957) of the freshwater sponges. University of South Carolina Publications, III, 3 (1): 1-97.

Penney, J. T. and A. A. Racek. 1968. Comprehensive Revision of a World-wide collection of freshwater sponges (Porifera: Spongillidae). United States National Museum Bulletin 272, 184 pp.

Poirrier, M. A. 1974. Ecomorphic variation in gemmoscleres of *Ephydatia fluviatilis* Linnaeus (Porifera: Spongillidae) with comments upon its systematics and ecology. Hydrobiology 44 (4): 337-447.

Poirrier, M. A. 1976. A taxonomic study of the *Spongilla alba, S. cenota, S. wagneri* species group (Porifera: Spongillidae) with ecological observations of *S. alba*. Pages 203-213 *in*: F. W. Harrison and R. R. Cowden, eds. Aspects of Sponge Biology. Academic Press, New York.

Potts, E. 1880a. Freshwater sponges of Fairmont Park. Proceedings of the Academy of Natural Sciences of Philadelphia, 32: 330-331.

Potts, E. 1880b. On freshwater sponges. Proceedings of the Academy of Natural Sciences of Philadelphia 32: 356-357.

Potts, E. 1881a. Some new genera of freshwater sponges. Proceedings of the Academy of Natural Sciences of Philadelphia 33: 149-150.

Potts, E. 1881b. A new form of freshwater sponge. Proceedings of the Academy of Natural Sciences of Philadelphia 33: 176.

Potts, E. 1882. Three more freshwater sponges. Proceedings of the Academy of Natural Sciences of Philadelphia 34: 12-14.

Potts, E. 1884. On the wide distribution of some American sponges. Proceedings of the Academy of Natural Sciences of Philadelphia 1884: 215-217.

Potts, E. 1885a. A new freshwater sponge from Nova Scotia. Proceedings of the Academy of Natural Sciences of Philadelphia 37: 28-29.

Potts, E. 1885b. Freshwater sponges from Mexico. Proceedings of the United States National Museum 8: 587-589.

Potts, E. 1886. Freshwater sponges from Newfoundland: a new species. Proceedings of the Academy of Natural Sciences of Philadelphia 38: 227-230.

Potts, E. 1887. Contributions towards a synopsis of the American forms of freshwater sponges with descriptions of those named by other authors and from all parts of the world. Proceedings of the Academy of Natural Sciences of Philadelphia 39: 158-279.

Potts, E. 1889. Report upon some freshwater sponges collected in Florida by Jos. Wilcox, Esq. Transactions of the Wagner Free Institute of Science. 2: 5-7.

Volkmer-Ribeiro, C. 1973. Redescription and ecomorphic variations of the freshwater sponge *Trochospongilla minuta* (Potts 1887). Proceedings of the Academy of Natural Sciences of Philadelphia 125(8): 137-144.

Volkmer-Ribeiro, C. 1976. A new monotypic genus of Neotropical freshwater sponges (Porifera: Spongillidae) and evidence of a speciation via Hybridism. Hydrobiologia 50 (3): 271-281.

Volkmer-Ribeiro, C. 1981. Porifera. Pages 86-95 *in* S. H. Hurlbert, G. Rodriguez and N. D. dos Santos eds. Aquatic Biota of Tropical South America, Part 2: Anarthropoda. San Diego State University, San Diego, California.

Volkmer-Ribeiro, C. 1986. Evolutionary study of the freshwater spong.e genus *Metania* Gray 1867: III. Metaniidae, new family. Amazoniana 9(4): 493-509.

Volkmer-Ribeiro, C. In press. A new insight into the systematics, evolution, and taxonomy of freshwater sponges. *In* K. Rützler and W. D. Hartman, eds. New Perspectives in Sponge Biology. Smithsonian Institution Press, Washington.

Volkmer-Ribeiro, C. and S. B. Maciel. 1983. New Freshwater sponges from Amazonian Waters. Amazoniana 8 (2): 255-264.

Volkmer-Ribeiro, C. and R. De Rosa-Barbosa.. 1985. Redescription of the freshwater sponges *Trochospongilla repens* (Hinde 1888) and *Trochospongilla amazonica* (Weltner 1895) with an account of the South American species of *Trochospongilla* (Porifera: Spongillidae). Iheringia, Série Zoologia, 65: 77-93.

Proceedings of The Academy of Natural Sciences of Philadelphia 139: 243-259, 1987

The avifauna of the Cordillera de Cutucú, Ecuador, with Comparisons to other Andean Localities

MARK B. ROBBINS AND ROBERT S. RIDGELY
Department of Ornithology
Academy of Natural Sciences, Philadelphia PA 19103

THOMAS S. SCHULENBERG
Museum of Natural Sciences, Louisiana State University
Baton Rouge LA 70803

FRANK B. GILL
Department of Ornithology
Academy of Natural Sciences, Philadelphia PA 19103

ABSTRACT.—The avifauna at four sites on the western slope of the Cordillera de Cutucú was surveyed in 1984. A list of bird species recorded by us along an elevational gradient (1000-2300 m), with an indication of relative abundance is given. Information is presented on the status, behavior, and habitat preferences of 12 poorly known species. A comparison of our findings with those from two other sites on the eastern Andes (Cordillera del Condor and Cerro Chinguela), reveals that the subtropical avifaunas are very similar among these sites.

Recent ornithological surveys of semi-isolated ridges lying east of the main Andes in Peru have yielded several previously undescribed taxa of birds (e.g., Fitzpatrick et al. 1977, Fitzpatrick and O'Neill 1979, Fitzpatrick and O'Neill 1986). The Cordillera de Cutucú, lying east of the main Andes in southeastern Ecuador, is an example of one of these semi-isolated ranges. Except for a narrow corridor (elevations of this connection appear to be less than 1500 m) that connects the northern end of the Cutucú to the main chain of the Andes, this range is completely isolated (see Fig. 1). Ornithologically the area is essentially unknown except for the work of the commercial collector L. Gomez, who made a small collection there and around the town of Macas some 50 years ago. From 2-5 August 1979 Ridgely, R.A. Rowlett and R. Hubert made observations on the lower west slope to the east of Macas.

In April of 1984, N. Krabbe of the Zoologisk Museum Copenhagen, Denmark, briefly visited the west slope and crest east of Logroño. From 10 June to 19 July 1984, an expedition mounted by the Academy of Natural Sciences, Philadelphia and Museo Ecuatoriano de Ciencias Naturales, Quito, surveyed the west slope and the crest of the Cutucú east and south of Logroño. We here present behavioral and distributional information on some poorly-known species, as well as a complete species list for each of the four localities surveyed within the Cutucú. We compare our findings with those from the Cordillera del Condor, another spur of the eastern Andes, and Cerro Chinguela, a nearby site on the eastern slope of the main Andean chain.

Sites and Methods

Taxonomy follows the American Ornithologists' Union Check-list of North American Birds (1983) and Meyer de Schauensee (1970), unless noted otherwise. Study skins are deposited at the Academy of Natural Sciences, of Philadelphia (ANSP), Museo Ecuatoriano de Ciences Naturales (MCN), in Quito, Ecuador, and Zoologisk Museum Copenhagen, Denmark. Frozen tissue samples are deposited at Louisiana State Museum of Zoology (LSUMZ), Baton Rouge, and anatomical specimens are at the U.S. National Mus. of Nat. Hist. (USNM), Smithsonian. Photographs of birds, vegetation, and camp sites are housed in the VIREO collection at ANSP (Myers et al.1986).

Four sites were surveyed, with the first two (1,2) located along the trail that runs from Logroño, a small town situated on the western slope of the Cutucú in the Río Upano valley, to Yaupi, a village on the eastern base of the Cutucú. The last two camps (3,4) were south of the above trail, on a trail cut by us.

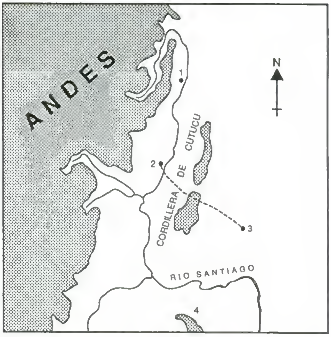


FIG. 1. Cordillera de Cutucú and Andes of southeastern Ecuador. 1, Macas; 2, Logroño; 3, Yaupi; 4, Cordillera del Condor. Shaded area represents elevations above 2000 m. Dashed line indicates approximate location of trail between Logroño and Yaupi.

Camp 1.— Río Chiguasa; 1075m; ca. 2°39' S, 78° 8' W; 13-22 June 1984. This camp was located on the lower west slope of the Cutucú along the trail that leads from Logroño to Yaupi (Fig. 1). The camp was sandwiched between two steep slopes along a stream locally named the "Río Chiguasa". This stream appears to be synonymous with the "Río Chiviaza", as reported in the New York Botanical Garden's expedition into this same area in 1944 (see map, p. 7 in Camp 1952). Netting was concentrated in the narrow, relatively flat area adjacent to the stream, although some netting was done along the slope above camp (up to 1200 m). Occasional forays were made along the trail up to 1325 m. The forest from the Chiguasa camp and up to the crest was pristine. Human disturbance was limited to the narrow trail (less than 1 m wide). Many of the trees along the Chiguasa were greater than 30 m in height, whereas the larger trees along the slopes were generally less than 20 m. Most of the trees were laden with epiphytes (VIREO # RO8-4-14,19,20). Bamboo was scarce at this camp. In our list for this camp, we include species recorded at a small farm settlement surrounded by undisturbed forest just below the camp at 1000 m (VIREO # RO8-4-4,5,15).

Camp 2.—"Yapitya;" 1700 m; 22 June-3 July 1984. This camp was located along the main trail. It was situated in a relatively flat area along a ridge top. Netting was restricted to the immediate camp area. However, our survey here included daily forays along the trail between ca. 1500-1800 m, occasionally to the trail crest at 2100 m. One small clearing (ca. 0.5 hectare) was present near our camp. Along the southern side of this ridge the canopy was relatively open with numerous tree falls and a dense understory. This may have resulted from winds associated with a storm that passed through this region a few months prior to our investigation. No extensive stands of bamboo were present.

Camp 3.— Southern Ridge, 1975 m; 3-10 July 1984. Prior to this camp, all of our work had been concentrated along the narrow trail that runs from Logroño to Yaupi. However, our goal was to survey the avifauna at the highest elevation possible. A broad ridge was visible from our "Yapitya" camp (VIREO # RO8-4-13), that clearly was higher in elevation than the crest where the main trail passed over to Yaupi. Therefore, while working at "Yapitya", we had our workers cut a new trail to the southern ridge. Camp # 3 was located at the saddle of a knife-like ridge. The vegetation was similar to our two previous camps. The forest became very stunted and wetter along the ridge just above our camp, with the ground and most of the vegetation covered with moss. Our work at this camp was concentrated from 1950 to 2100 m.

Camp 4.— Elfin Forest Camp. 2225 m; ca. 2° 43' S, 78°5' W; 10-17 July 1984. This camp was located on the top of a knife-like ridge. Nearly all of the vegetation was covered with moss and all trees were laden with epiphytes (VIREO # RO8-4- 1,2,6,7,8,11,18). Extensive stands of bamboo were visible from our camp on a slope immediately to the south. It was windy and rain fell several times each day. Most of the time we were enshrouded in clouds. All of our work was conducted between 2100-2300 m along the ridge top.

SPECIES ACCOUNTS

Leucopternis princeps

Barred Hawk

We encountered 1-3 individuals daily at our 1975 and 2225 m camps, with one bird observed as low as 1200 m. Birds were recorded giving a single-noted whistle ca. 1 sec. in duration. Chapman (1926) lists *L. princeps* for eastern and western Ecuador, although all of his specific localities are for the western slope. We know of only two records for the eastern slope of the Ecuadorian Andes: a specimen (Am. Mus. Nat. Hist., AMNH, 178948), from San Jose de Sumaco, Prov. Napo, and a sight record by Ridgely of a pair at Coca Falls, Prov. Napo (1250 m) on 14 June 1985.

Pyrrhura melanura and P. albipectus

Maroon-tailed & White-breasted Parakeets

Several flocks, consisting of 4-10 birds each, were encountered from 1000 to 1700 m. Birds observed in flocks at the edge of primary forest at 1000 m consistently appeared to differ morphologically from individuals seen between 1200-1700 m. At least four individuals, one of which was collected (ANSP 176701), of a flock of eight birds at 1000 m most closely matched *P. melanura berlepschi*. Additional flocks in this same area appeared to be comprised primarily of birds of similar plumage though there were some individuals with white to yellow breasts which had only faint dark barring or completely lacked it. We are unsure whether these different morphological types represented age classes of one species or hybrids between *melanura* and *P. albipectus*. All birds seen between 1200 and 1700 m (two of which were collected, ANSP 176700, Zoologisk Mus. Copenhagen 80000) appeared to be typical *albipectus*. An alternative explanation may be that *melanura* and *albipectus* are separated elevationally (*melanura* in the the tropical and upper tropical zones, *albipectus* in the subtropical zone) during the breeding season, but form mixed-species flocks at other periods of the year.

Nystalus striolatus

Striolated Puffbird

One to three individuals were heard daily from 1200 to 1700 m. Chapman (1926) lists only one record for Ecuador (Prov. Pastaza, Sarayacu). Apparently, our specimens (ANSP 176708, 177167) represent the second record for the country. This species was found in widely separated pairs in the forest canopy, mostly near clearings and steep slopes. Based on available data, the elevations at which it was found on the

Cutucú were unusually high for it (elsewhere it is known only from the tropical lowlands). Likewise, we were surprised to collect *Bucco capensis*, *Deconychura longicauda*, and *Thamnophilus aethiops* at 1700 m. To our knowledge this is the highest elevation reported for these species.

Malacoptila fulvogularis

Black-streaked Puffbird

This species is easily overlooked unless the song is known. We encountered one to four individuals daily from 1525 to just below 2000 m. The song is a very high-pitched ascending whistle, ca. 3.75 sec in duration. The initial part of the song is reminiscent of the call of *Pipreola frontalis*, a species that overlaps *fulvogularis* in elevation from Ecuador to Bolivia. Puffbirds were observed singing from horizontal perches ca. 6-10 m above the ground. Although this species has been recorded at only two localities in Ecuador, Mapota and Macas (Chapman 1926, Ridgely unpubl.), it undoubtedly occurs at appropriate elevations along the entire eastern slope of the Ecuadorian Andes.

Grallaria haplonota

Plain-backed Antpitta

Prior to our investigation of the Cordillera de Cutucú, this species was unrecorded from the eastern slope of the Andes. Thus we were surprised to find this species to be present in small numbers in the forest between 1625 and 1700 m. Three males were collected and represent a new race, *G. h. chaplinae* (Robbins and Ridgely 1986).

Chloropipo unicolor

Jet Manakin

This species was captured almost daily in our mist nets at 1700 m, where it was evidently quite numerous. There is only one previous record of this species for Ecuador. Ridgely (1980) collected a female specimen (AMNH 824232) from the upper Río Upano valley on 30 July 1979 (1550 m), on the eastern slope of the Andes approximately opposite the Cutucú. However, two other unpublished specimens (Museum of Comparative Zoology, Harvard (MCZ) 329699, male, 7 August 1964; MCZ 329700, female, 11 August 1964) were taken by D. Norton at Palm Peak, on the southeast slope of Volcán Sumaco, Prov. Napo, the northernmost locality at which the species has been found. We rarely observed this species out of the mist-nets; its habits remain virtually unknown. Further study will probably show that *C. unicolor* is continuously distributed at appropriate elevations (probably centering on 1500-1700 m) along much of the east slope of the Ecuadorian Andes.

Phylloscartes superciliaris

Rufous-browed Tyrannulet

Prior to our investigation this species had never been found on the eastern slope of the Eastern Andes. The nearest known locality is Virolín, Santander, on the western slope of the northern Eastern Andes in Colombia (Hilty & Brown 1983; note that this is incorrectly stated to be on the western slope of the Central Andes in Paynter and Traylor 1981), ca.1150 km north of the Cordillera de Cutucú; however, there are specimens from "Bogotá", opening the possibilty that this species' range is not disjunct along the eastern slope of the Andes. We found it to be fairly common (one to six individuals recorded daily), in mid-level and canopy mixed-species flocks. Individuals were observed making short (less than 1 m) sally gleans to leaves and branches for insects. When perched, birds sat with the body tilted forward, ca. 25°< from the vertical. Somewhat surprisingly (if indeed the range is disjunct), our four specimens do not appear to be racially distinct from birds collected in northern Colombia and western Venezuela; in fact, all three described races are very weakly differentiated: *superciliaris* (Costa Rica and western Panama), *palloris* (eastern Panama), *griseocapillus* (northern Colombia and western Venezuela).

Phylloscartes gualaquizae

Ecuadorian Tyrannulet

This little-known flycatcher was observed regularly at ca. 1000 m making short (less than 1 m) sally gleans to leaves and branches while accompanying mixed-species flocks 10-30 m above the ground. One bird was heard to sporadically give a thin "feeee" call. Traylor (1977) merged the genus *Pogonotriccus*, in which this species was placed, into *Phylloscartes*. We follow this merger here, but on the Cutucú discovered that *gualaquizae* exhibits markedly different behavior from other members of "*Pogonotriccus*." The latter (e.g., *ophthalmicus*, *poecilotis*, etc.) tend to exhibit a very different posture from typical *Phylloscartes* (e.g., *ventralis*, *superciliaris*), perching more or less upright with the tail held vertically, but *gualaquizae* perched with the body tilted forward (ca. 30°< from the veritcal), and held its tail partially cocked. Thus it resembles other typical *Phylloscartes*. We are not certain whether the merger of these two genera is correct; in any case it obscures the fact that there exists a striking behavioral dichotomy within it. *P. qualaquizae* is known only from the upper tropical and subtropical zones on the east slope of the Andes in eastern Ecuador and northern Peru (Dept. San Martín), and is known from very few specimens; we obtained two (ANSP 176931,176932).

Platyrinchus flavigularis

Yellow-throated Spadebill

Although this species is recorded from Venezuela to central Peru (Meyer de Schauensee 1970), it is known from only a single unpublished locality in Ecuador. Norton collected a pair (MCZ 329507, 329500) at Palm Peak (1500 m), on the southeast slope of Volcán Sumaco, Prov. Napo on 6 August 1964. Another individual (MCZ 32950) was taken by Norton on 9 August 1963, near the above locality at the head of the Río Guataracu (ca. 750 m). We do not know the basis for Meyer de Schauensee's (1966) inclusion of its being recorded from "northeastern Ecuador", as he did not know of the Norton collection. We found it to be fairly common, 1-2 individuals observed daily, between 1500-1700 m. Typically, birds were encountered in pairs perched 4-8 m above the ground. As with other spadebills, they did not associate with mixed-species flocks. Both sexes were recorded giving a short, single-noted squeak, not unlike the sound produced from squeezing a rubber toy.

Myiophobus roraimae

Roraiman Flycatcher

Our specimen (ANSP 176961), apparently represents the first for Ecuador. This specimen is similar to the type (ANSP 101730) of *M. r. rufipennis* and eight other specimens from Peru (Dept. San Martín, Huánuco, Pasco, and Ayacucho: LSUMZ). Two apparent family groups (3-4 individuals/group) were observed at 1700 m at the edge of small forest clearings. Individuals were observed making short (<1 m) sally gleans to leaves and branches from ca. 2 to 7 m above the ground. Behaviorally, *M. roraimae* is similar to other forest-inhabiting species of the genus *Myiophobus* (e.g., *flavicans*), though Lanyon (1986) suggests that based on cranial characters it may be generically distinct.

Chlorospingus parvirostris

Short-billed Bush-Tanager

Considerable confusion exists regarding the occurrence of this species in Ecuador. Zimmer (1947, p. 8), mentions Taczanowski and Berlepsch's (1885) records of the species from Mapoto and Machay, but Meyer de Schauensee (1966, p. 493) records it only from the latter, while Storer (1970, p.260) specifically states "not recorded from Ecuador, where it probably occurs". We do not know whether he overlooked the early records, or if they are invalid. In any case, D. Norton collected three specimens (MCZ 299768, 299765, 299766) along the Zamora road (km 45), Prov. Zamora-Chinchipe, during late August and September 1965, and we collected a single specimen (ANSP 177053) on the Cutucú at 2100m.

Otherwise it has not been recently recorded in

Ecuador, where it appears to be rare or perhaps very local.

Saltator cinctus
Masked Saltator

This rarely encountered species was observed twice. A single bird responded to squeaking along a ridge top covered with elfin forest at 2100 m on 4 July. The bird was recorded giving a high pitched sharp, emphatic "tseeyk!" On 12 July, at 2275 m, Robbins observed another individual giving a loud, single-noted "chu" repeated at ca. 3-5 sec intervals. The call (reminiscent of *Cyanolyca virdicyana* calls) was delivered from the top of a slim tree (ca. 15 cm) along a ridge top at dusk. This species is known from fewer than 12 specimens (O'Neill & Schulenberg 1979). The type, AMNH 748391, was also taken in the Cutucú at ca. 2000 m on 28 Dec 1940; this still represents the only known locality for the species in Ecuador.

AVIFAUNAL COMPARISONS OF THE CORDILLERAS

Recent avifaunal surveys of spurs of the eastern Andes in Ecuador and northern Peru now permit initial comparisons among these semi-isolated cordilleras, and with the main Andean chain. These comparisons may reveal distributional patterns of Andean birds and may offer insights into the dispersal abilities of some of these montane birds. We compare our Cutucú findings (Appendices I and II) with those from a site at the southern tip of the Cordillera del Condor (ca. 260 km from our Cutucú sites), another spur of the eastern Andes, lying directly to the south of the Cutucú (Fig. 1). The Río Santiago separates the two cordilleras. In addition, the avifaunas of these two sites are compared with an intensively investigated site (Cerro Chinguela, ca. 300 km SSW of the Cutucú sites surveyed), on the main Andean chain. The Condor was explored in June 1975 and July 1976, by field parties from Princeton University (J. Fitzpatrick, D. Willard, J. Terborgh et al.) and the Louisiana State Univ. Museum of Zoology (J.P. O'Neill, G.R. Graves). Parker et al. (1985) give details of the Chinguela survey. The areas that were surveyed in the Condor and Cutucú are nearly identical in maximum elevation (ca. 2400 m) and similar in overall topography, whereas maximum elevations at Cerro Chinguela are considerably higher (3350 m). The Condor/Cutucú comparison is limited to elevations above 1900 m, as field work in the Condor was concentrated above that elevation (Fitzpatrick and Graves, pers. comm.). Only the west slopes and the crests of the Condor and Cutucú were investigated, and to insure comparability between the Cutucú and Cerro Chinguela, birds found exclusively above 2400 m on Chinguela are excluded.

The Cutucú/Condor comparison is presented in Table 1. Listed under each locality are species not recorded at the other site. At first glance these lists appear to have a relatively high number of "unique" species, i.e., species not recorded at both localities; however, both lists include species that likely were present in the other range, but which for a variety of reasons were not found. For example, extensive stands of bamboo and open, grassy habitats were extremely limited in the Cutucú. We did not adequately survey these habitats, and doubtless in large part as a result, several species were unrecorded (*Colibri thalassinus, Lesbia nuna, Synallaxis azarae,* and *Haplospiza rustica*), all of which are elsewhere known to be found mostly or entirely in bamboo patches or grassy habitats. Several species in the above lists occur in low densities and/or are very inconspicuous, thus are easily overlooked, e.g., *Malacoptila fulvogularis, Pipreola lubomirskii, Lipaugus cryptolophus, Knipolegus signatus, K. poecilurus* and the *Saltator cinctus*. Additionally, the fact that a *Grallaria* was missing from each list may be an artifact of having sampled these sites during the non-breeding (non-vocal) period. More extensive sampling is needed to determine whether the above absences are real.

We feel that those species marked with an asterisk were actually absent from the other site, and not simply missed due to sampling errors. When a comparison is made between the two sites from this pool of missing species, it turns out that about 10.5 % (n =114 species) of the Condor and about 9 % of the Cutucú avifauna is unique (i.e., not shared with the other locality). The reasons for these differences may lie in the notable (and surprising) contrasts between the soil and vegetation at the two sites. The west slope of the Condor is apparently drier and the soil is more porous and sandier than in the Cutucú and Chinguela sites (see Fitzpatrick et al. 1977). This is reflected in the relative diversity of the vegetation, as Fitzpatrick et al. (1977) noted the vegetation appears more depauperate in the Condor than at other eastern slope sites in Peru. In contrast, the Cutucú is extremely wet and floristically diverse. We quote W.H. Camp (1952), a botantist who visited the Cutucú in 1944, "... but to me it [Cutucú] stands out as the floristically richest small range I have ever studied. This, in my opinion, is the result of the high humidity, the geological background, and constant disturbance [natural] of the vegetation."

The absence of _Leucopternis occidentalis_ and _Atlapetes leucopterus_ in the Cutucú is thus not surprising, for these species prefer relatively less humid situations. The absence of _Atlapetes rufinucha_ in the Cutucú further supports

Table 1. Condor/Cutucú avifaunal comparisons (ca. 1900-2400 m). Listed under each locality are species "unique" to that site. Species marked with an asterisk are considered to be absent from the other site (see text). The combined species total for both sites at the above elevation is about 114.

Condor	Cutucú
*_Leucopternis occidentalis_	*_Leucopternis princeps_
Aegolius harrisii	_Columba fasciata_
Caprimulgus longirostris	_Geotrygon frenata_
Doryfera ludoviciae	*_Haplophaedia aureliae_
Colibri thalassinus	_Malacoptila fulvogularis_
*_Heliangelus regalis_	_Eubucco bourcierii_
Lesbia nuna	_Aulacorhynchus prasinus_
Synallaxis azarae	_Margarornis squamiger_
*_Syndactyla rufosuperciliata_	_Premnornis guttuligera_
Grallaria ruficapilla	_Syndactyla subalaris_
*_Ampelion rubrocristatus_	_Grallaria hypoleuca_
Elaenia obscura	_Pipreola lubomirskii_
Knipolegus signatus	_Lipaugus cryptolophus_
Knipolegus poecilurus	*_Mecocerculus minor_
*_Anthus bogotensis_	*_Pseudotriccus pelzelni_
*_Henicorhina leucoptera_	*_Pseudotriccus ruficeps_
*_Cistothorus platensis_	*_Hemitriccus granadensis_
*_Tangara viridicollis_	*_Myiophobus flavicans_
*_Iridosornis rufivertex_	*_Ochthoeca diadema_
*_Cnemoscopus rubrirostris_	*_Myiotheretes fumigatus_
*_Atlapetes rufinucha_	*_Pachyramphus versicolor_
*_Atlapetes leucopterus_	_Troglodytes solstitialis_
Haplospiza rustica	_Tangara vassorii_
	Saltator cinctus

Paynter's assertion (1978) that the gap of ca. 250 km along the eastern slope of Ecuador, between Papallata, Prov. Napo, and the Prov. of Azuay is real and not an artifact of collecting. Unexpected was the absence of the *Heliangelus regalis* and the *Henicorhina leucoptera* from the Cutucú, since both have been recorded both north and south of the Río Marañón in wet, stunted forest similar to that found at appropriate elevations in the Cutucú. The presence of temperate zone species such as *Ampelion rubrocristatus, Cistothorus platensis, Anthus bogotensis, Cnemoscopus rubrirostris,* and *Iridosornis rufivertex* in the Condor may be related to the fact that the ridge surveyed by Fitzpatrick et al. is linked much higher ridge that exceeds 2850 m, whereas the Cutucú is separated from higher elevations of the eastern Andes. All of the above temperate zone species were also recorded on Chinguela, but only at elevations well above that surveyed in the Cutucú (thus, these species are excluded from the pool of species missing in the Cutucú/Chinguela comparison).

Interestingly, *Haplophaedia aureliae,* which was a fairly common bird in the Cutucú, was not recorded on either the Condor or at Chinguela. We are at a loss to explain its absence from these sites. Eight remaining species missing from the Condor, were flycatchers (seven of which were relatively common) in wet, stunted forest along

Table 2. Cutucú/Chinguela avifaunal comparisons (ca. 1700-2400). Listed under each locality are species "unique" to that site. This comparison excludes species recorded between 1700 and 2400 m at the Chinguela site that are obvious temperate zone species. Species marked with an asterisk are considered to be absent from the other site (see text). The combined species total for both sites at the above elevation is about 153.

Cutucú	Chinguela
Leucopterus princeps	*Buteo polyosoma*
Odontophorus speciosus	*Claravis mondetoura*
Columba subvinacea	*Aegolius harrisii*
Steatornis caripensis	*Camprimulgus longirostris*
Phaethornis guy	*Lurocalis rufiventris*
**Haplophaedia aureliae*	*Colibri thalassinus*
Eubucco bourcierii	**Helidoxa rubinoides*
Veniliornis dignus	*Chalcostigma ruficeps*
Lipaugus cryptolophus	*Acestrura mulsant*
Zimmerius viridiflavus	*Synallaxis azarae*
Catharus dryas	**Syndactyla rufosuperciliata*
	Grallaria ruficapilla
	Chamaeza mollisima
	Phyllomyias plumbeiceps
	Mecocerculus calopterus
	**Leptopogon rufipectus*
	**Contopus fumigatus*
	Knipolegus poecilurus
	**Catharus fuscater*
	**Tangara ruficervix*
	**Tangara viridicollis*
	Hemispingus frontalis
	**Atlapetes rufinucha*
	**Atlapetes leucopterus*

ridge tops in the Cutucú. This habitat was adequately surveyed by observers using mist-nets at similar elevations in the Condor (Fitzpatrick, Graves, pers. comm.), and we cannot explain their absence there. Perhaps this is another reflection of the low-diversity, stunted forest atop the Condor (Fitzpatrick, pers. comm.)

All of the species which we feel were actually absent from the Condor, but were present in the Cutucú (with the exception of the *Leucopternis princeps*), have been recorded at Chinguela, as well as south of the Río Marañón on the eastern slope of the eastern Peruvian Andes. In fact, a Cutucú/Chinguela comparison reveals that only one or two species (1 %, n=ca. 153 species; see Table 2) occurs in the Cutucú and not at Chinguela. However, about 7 % of the Chinguela species total (n =142 species, 1700-2400 m) were actually missing from the Cutucú. The Cutucú and Chinguela sites share at least seven species that are unrecorded for the Condor, whereas the Condor and Chinguela sites share five species not found in the Cutucú. Of these five species, the *Syndactyla rufosuperciliata*, *Tangara viridicollis*, and *Atlapetes leucopterus* are unknown from the eastern slope of Ecuador. At least three species (*Heliangelus* and *Henicorhina*) recorded from the Condor, are unknown from either of the other two localities.

In summary, the subtropical avifaunas differ only slightly among these three sites. The composition of the Cutucú/Chinguela avifaunas is particularly similar. The minor differences between the Condor avifauna and the other two sites may be a reflection of the differences in soils and vegetation among sites.

ACKNOWLEDGMENTS

We wish to express our deep appreciation to the members of the Catherwood family, who through the Catherwood Foundation made our exploration of the Cordillera de Cutucú possible. We sincerely thank Miguel Moreno of the Museo Ecuatoriano de Ciencias Naturales, Quito, and the Ministerio de Agricultura, Quito for support and authorization of our research. J. Fitzpatrick, G. Graves, and D. Willard kindly provided information on their expedition into the Condor. Fitzpatrick and Graves also made helpful comments on the manuscript. We are grateful to N. Krabbe for information from his visit into the Cutucú. The following people and institutions kindly provided access to specimens and other materials under their care: J. Gulledge (Cornell Lab. of Sound, Univ. of Cornell), M. LeCroy (AMNH), R.A. Paynter, Jr. (MCZ) and J.V. Remsen, Jr. (LSUMZ). We are indebted to Todd Miller for his dedicated assistance, which made this expedition possible. P. and M. Greenfield kindly provided welcome hospitality. G. Glenn kindly produced the figure. We thank J. Espinosa, G. Glenn, P. Greenfield, S. Greenfield, and R. Peck for help and companionship during our field work.

LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds. 6th ed., Allen Press, Lawrence, Kansas.

CAMP, W.H. 1952. Plant hunting in Ecuador. Memoirs of New York Botanical Garden. 8: 1-24.

CHAPMAN, F. M. 1926. The distribution of bird-life in Ecuador. Bull. Am. Mus. Nat. Hist. 60: 1-784.

FITZPATRICK, J. W., J. W. TERBORGH, AND D. W. WILLARD. 1977. A new species of wood-wren from Peru. Auk 94: 195-201.

FITZPATRICK, J. W. AND J. P. O'NEILL. 1979. A new Tody-tyrant from northern Peru. Auk 96: 443-447.

FITZPATRICK, J. W. AND J. P. O'NEILL. 1986. *Otus petersoni*, a new screech-owl from the eastern Andes, with systematic notes on *O. colombianus* and *O. ingens*. Wilson Bull. 98: 1-14.

FJELDSÅ, J. AND N. KRABBE. 1986. Some range extensions and other unusual records of Andean birds. Bull. Brit. Ornith. Club. 106:115-124.

HILTY, S. L. AND W. L. BROWN. 1983. Range extensions of Colombian birds as indicated by M. A. Carriker, Jr. collection of the National Museum of Natural History, Smithsonian Institution. Bull. Brit. Ornith. Club. 103:5-18.

LANYON, W. E. 1986. A phylogeny of the thirty-three genera in the *Empidonax* assemblage of tyrant flycatchers. Am. Mus. Novitates No. 2846.

MEYER DE SCHAUENSEE, R. 1966. The species of birds of South America and their distribution. Livingston Publ. Co., Narberth, Pennsylvania.

MEYER DE SCHAUENSEE, R. 1970. A guide to the birds of South America. Livingston Publ. Co., Wynnewood, Pennsylvania.

Myers, J. P., R. F. Cardillo, and F. B. Gill. 1986. VIREO: procedures and services for the ornithological community. Condor 88: 115-117.

O' Neill, J. P. and T. S. Schulenberg. 1979. Notes on the Masked Saltator, *Saltator cinctus*, in Peru. Auk 96: 610-613.

Parker, T. A., III, T. S. Schulenberg, G.R. Graves, and M. J. Braun. 1985. The avifauna of the Huancabamba region, northern Peru. Pp. 169-197 in "Neotropical Ornithology" (P. A. Buckley et al., eds.), Ornithol. Monogr. No. 36.

Paynter, R. A., Jr. 1978. Biology and evolution of the avian genus *Atlapetes* (Emberizinae). Bull. Mus. Comp. Zool. 148: 323-369.

Paynter, R. A., Jr. and M. A. Traylor. 1981. Ornithol. Gazetteer of Colombia. Harvard Univ. Press, Cambridge, Massachusetts.

Ridgely, R. S. 1980. Notes on some rare or previously unrecorded birds in Ecuador. Am. Birds. 34: 242-248.

Ridgely, R.S. and G. Tudor. in prep. Birds of South America; Furnariidae-Cotingidae. Univ. Texas Press.

Robbins, M. B. and R. S. Ridgely. 1986. A new race of *Grallaria haplonota* (Formicariidae) from Ecuador. Bull. Brit. Ornith. Club. 106: 101-104.

Schulenberg, T. S. and F. B. Gill. 1987. First description of the nest of the Olive Finch, *Lysurus castaneiceps*. Condor 89: 673-674.

Storer, R. W. 1970. Thraupinae. Pp. 246-408. In R. A. Paynter, Jr. (ed.), Check-list of the Birds of the World, Vol. 13. Mus. of Comp. Zool., Cambridge, Massachusetts.

Taczanowski, L. and H. von Berlepsch. 1885. Troisieme list des oiseaux recueillis par M. Stolzmann dans l'Ecuadeur. Proc. Zool. Soc., London.

Traylor, M. A., Jr. 1977. A classification of the tyrant flycatchers (Tyrannidae). Bull. Mus. Comp. Zool. 148:129-184.

Zimmer, J. T. 1947. Studies of Peruvian birds. 52. The genera *Sericossypha, Chlorospingus, Cnemoscopus, Hemispingus, Conothraupis, Chloronis, Lamprospiza, Cissopis,* and *Schistochlamys*. Am. Mus. Novit. No. 1367.

APPENDIX 1

Relative abundances for bird species recorded in the Cordierra de Cutucú[1]

	River Camp a	Yapitya Camp b	1975 m Camp c	2225 m Camp d
Crypturellus soui	U			
Nothocercus bonapartei		R		
Tigrisoma fasciatum	X			
Coragyps atratus		X		
Cathartes melambrotos	X			
Chondrohierax uncinatus			X	
Elanoides forficatus	X	U		
Harpagus bidentatus	X	U		
Ictinia plumbea	U			
Buteo magnirostris	X			
Buteo albigula				X
Buteo brachyurus	X			X
Leucopternis princeps	X		U	U
Oroaetus isidori	X		X	
Micrastur ruficollis		U	R	
Falco rufigularis	X			
Chamaepetes goudotii	X			
Odontophous speciosus	X	X	X	
Columba fasciata				X
Columba subvinacea	FC	FC	FC	
Geotrygon saphirina	X			
Geotrygon frenata	X	FC	FC	
Aratinga leucophthalmus	FC			
Pyrrhura albipectus	U			
Pyrrhura melanura	U			
Touit stictoptera		FC		
Pionus sordidus		U	U	U
Amazona mercenaria			FC	U
Piaya cayana	FC	FC	FC	
Crotophaga ani	X			
Otus ingens		U		X
Otus petersoni [2]			X	X
Glaucidium jardinii		FC	FC	
Ciccaba albitarsus			U	U
Steatornis caripensis				R
Streptoprocne zonaris	FC	FC	FC	U
Cypseloides rutilus	FC	FC		
Chaetura cinereiventris	FC	FC		
Chaetura brachyura	U			
Doryfera johannae	X			
Glaucis hirsuta	U			
Threnetes leucurus	FC			
Phaethornis guy	C	FC		

APPENDIX 1 Cont.

Phaethornis syrmatophorus	U	U	X	
Phaethornis superciliosus	X			
Phaethornis griseogularis	U	X		
Eutoxeres aquila	U	X		
Eutoxeres condamini	U			
Campylopterus villaviscensio	U	U		
Klais guimeti		U		
Thalurania furcata	FC	U		
Taphrospilus hypostictus	X			
Adelomyia melanogenys		FC	FC	FC
Urosticte benjamini		X	X	
Phlogophilus hemileucurus	U			
Heliodoxa leadbeateri	FC	FC	X	
Coeligena coeligena		FC	U	X
Coeligena torquata			FC	FC
Boissonneaua matthewsii			FC	
Heliangelus amethysticollis			FC	C
Haplophaedia aureliae		FC	FC	
Ocreatus underwoodii	FC	FC	FC	
Aglaiocercus kingi		U	U	X
Schistes geoffroyi	X	X		
Heliothryx aurita	R			
Trogon collaris	U			
Trogon personatus		U	FC	FC
Trogon curucui	X			
Pharomachrus antisianus		U	FC	
Pharomachrus auriceps [3]			X	X
Ceryle torquata	X			
Momotus momota	U	U		
Galbula pastazae		X		
Jacamerops aurea	U			
Bucco capensis		X		
Nystalus striolatus	U	U		
Malacoptila fulvogularis		U	U	
Micromonacha lanceolata	X			
Capito niger	U	X		
Eubucco bourcierii	U	FC	FC	
Aulacorhynchus derbianus	U	FC		
Aulacorhynchus prasinus			U	X
Ramphastos culminatus	FC			
Picumnus aurifrons	U			
Piculus rubiginosus	FC	FC		
Dryocopus lineatus	R			
Melanerpes cruentatus	FC			
Veniliornis fumigatus	U	U		
Veniliornis dignus		U	U	X
Campephilus haematogaster		U		

APPENDIX 1 cont.

Dendrocincla tyrannina			X	
Dendrocincla fuliginosa	U			
Deconychura longicauda		U		
Sittasomus griseicapillus	X			
Glyphorhynchus spirurus	C	FC	X	
Xiphocolaptes promeropirhynchus	X			X
Dendrocolaptes picumnus		X		
Xiphorhynchus triangularis	C	C	FC	
Lepidocolaptes affinis	U	X		
Campylorhamphus pusillus		U		
Synallaxis albigularis	U			
Synallaxis unirufa		X	U	FC
Cranioleuca curtata	FC	U		
Siptornis striaticollis			R	
Xenerpestes singularis	U	U		
Margarornis squamiger			R	U
Premnornis guttuligera			U	
Premnoplex brunnescens	FC	U	U	U
Pseudocolaptes boissonneautii			U	FC
Hyloctistes subulatus		U		
Syndactyla subalaris		FC	U	
Anabacerthia striaticollis	FC	FC		
Philydor rufus		FC		
Automolus dorsalis	X			
Thripadectes melanorhynchus	U	U		
Thripadectes sp.			X	
Xenops rutilans			U	X
Xenops minutus	X			
Sclerurus albigularis		X		
Thamnophilus schistaceus	U			
Thamnophilus aethiops		U		
Thamnophilus unicolor			U	
Thamnistes anabatinus	FC	FC		
Dysithamnus mentalis	U	FC		
Thamnomanes plumbeus		FC		
Myrmotherula haematonota	U			
Myrmotherula axillaris	X			
Myrmotherula schisticolor	U	FC		
Herpsilochmus axillaris	FC	U		
Drymophila caudata [3]		X		
Terenura callinota		FC		
Cercomacra nigrescens	X	U		
Pyriglena leuconota	U	U		
Percnostola leucostigma	X			
Pithys albifrons	U			
Hylophylax naevia	FC			
Hylophylax poecilonota	U			
Chamaeza campanisona	FC	U		

APPENDIX 1 cont.

Formicarius rufipectus	FC	FC		
Grallaria squamigera				X
Grallaria haplonota		U		
Grallaria hypoleuca			FC	FC
Grallaricula peruviana [4]				X
Conopophaga castaneiceps		FC		
Scytalopus unicolor			FC	C
Scytalopus femoralis		FC	U	
Zimmerius viridiflavus	FC	FC	FC	
Elaenia sp.			U	
Mecocerculus poecilocercus				X
Mecocerculus minor		X	FC	FC
Serpophaga cinerea	X			
Mionectes striaticollis		C	C	U
Mionectes olivaceus	C	U	X	
Leptopogon superciliaris	U			
Phylloscartes poecilotis		FC	R	
Phylloscartes ophthalmicus		FC	X	
Phylloscartes gualaquizae	U			
Phylloscartes superciliaris		U		
Pseudotriccus pelzelni			FC	
Pseudotriccus ruficeps				U
Lophotriccus pileatus	FC	FC		
Poecilotriccus capitale	U			
Hemitriccus sp.	1300 m			
Hemitriccus granadensis			FC	FC
Todirostrum cinereum	FC			
Rhynchocyclus fulvipectus	U			
Tolmomyias sulphurescens	U			
Platyrinchus flavigularis		U		
Platyrinchus mystaceus	U	U	X	
Myiotriccus ornatus	C	C	U	
Myiophobus flavicans			FC	FC
Myiophobus roraimae		U		
Myiophobus cryptoxanthus	X			
Pyrrhomyias cinnamomea	U	FC	FC	U
Ochthoeca diadema				FC
Myiotheretes fumigatus				FC
Colonia colonus	FC			
Myiarchus cephalotes	U	FC	X	
Myiozetetes similis	U			
Conopias cinchoneti	U	U	X	
Myiodynastes chrysocephalus	X	FC		
Tyrannus melancholicus	FC			
Pachyramphus versicolor			X	R
Pachyramphus viridis	FC	X		
Pachyramphus albogriseus		FC	X	
Tityra semifasciata	FC			
Pipreola riefferii			C	C

APPENDIX 1 cont.

Pipreola lubomirskii			U	
Pipreola frontalis		FC		
Pipreola chlorolepidota		X		
Ampelioides tschudii		R		
Lipaugus cryptolophus			R	
Cephalopterus ornatus	U			
Rupicola peruviana	U	U		
Schiffornis turdinus	U			
Chloropipo holochroa	U			
Chloropipo unicolor		FC		
Masius chrysopterus		U	X	
Pipra isidorei	U	U		
Notiochelidon cyanoleuca	FC			
Cyanocorax yncas		U	U	
Cinclus leucocephalus	X			
Campylorhynchus turdinus	FC			
Odontorchilus branickii		FC		
Cinnycerthia peruviana			FC	FC
Thryothorus genibarbis	U			
Troglodytes aedon	U			
Troglodytes solstitialis	X		U	U
Henicorhina leucosticta	FC			
Henicorhina leucophrys		FC	FC	FC
Cyphorhinus thoracicus	U			
Cyphorhinus arada	X			
Myadestes ralloides			FC	
Catharus dryas	X	FC		
Platycichla leucops	U	X		
Turdus serranus				U
Turdus fulviventris			U	
Vireo leucophrys	FC	FC	FC	
Hylophilus olivaceus	U	X		
Vireolanius leucotis	FC	FC		
Cyclarhis sp			FC	FC
Parula pitiayumi	FC	FC		
Myioborus miniatus	FC	C	FC	
Myioborus melanocephalus				FC
Basileuterus luteoviridis				X
Basileuterus tristriatus		C	FC	
Basileuterus coronatus		FC	FC	
Coereba flaveola	FC	U		
Conirostrum albifrons			U	X
Pipraeidea melanonota	X			
Chlorochrysa calliparaea	FC	FC	U	
Iridophanes pulcherrima		U	X	
Tangara velia	X			
Tangara chilensis	C	U		
Tangara schrankii	FC			
Tangara punctata	FC	U		

APPENDIX 1 cont.

Tangara xanthogastra	FC			
Tangara arthus	C	C	U	
Tangara xanthocephala		U	U	X
Tangara chrysotis	U	U		
Tangara parzudakii		FC	FC	X
Tangara cyanotis		FC	X	
Tangara cyanicollis	FC	U		
Tangara gyrola	C	U		
Tangara nigroviridis			FC	FC
Tangara vassorii				U
Iridosornis analis		U	FC	FC
Dacnis cayana	X			
Dacnis lineata	U			
Chlorophanes spiza	FC			
Cyanerpes caeruleus	FC			
Chlorophonia cyanea		U		
Chlorophonia pyrrhophrys				X
Euphonia xanthogaster	C	C	FC	
Euphonia mesochrysa		FC		
Anisognathus flavinucha	FC	FC	FC	X
Thraupis episcopus	FC			
Thraupis palmarum	FC			
Ramphocelus carbo	U			
Calochaetes coccineus		FC		
Piranga leucoptera	U	U		
Creurgops verticalis			U	
Chlorospingus ophthalmicus		X	FC	C
Chlorospingus flavigularis	C	FC		
Chlorospingus parvirostris			X	
Chlorospingus canigularis	FC	U		
Chlorornis riefferii			U	FC
Cissopis leveriana	X			
Catamblyrhynchus diadema				R
Saltator coerulescens	X			
Saltator maximus	FC			
Saltator cinctus				R
Pitylus grossus	FC	X		
Lysurus castaneiceps [5]	FC			
Atlapetes brunneinucha		FC	FC	FC
Arremon aurantiirostris	U			
Oryzoborus angolensis	X			
Diglossa caerulescens		FC	U	U
Diglossa albilatera			U	FC
Diglossa glauca	FC	FC		
Diglossa cyanea			FC	FC
Psarocolius angustifrons	FC	FC		
Cacicus uropygialis	FC	FC	U	
Carduelis olivacea	U			

[1] Abundances are given for bird species at the following localities: **River** = Camp a, Río Chiguasa, ca. 1075 m; **Yapitya** = Camp b, ca. 1700 m; **1975 m** = Camp c, Southern Ridge, ca. 1975 m; **2225 m** = Camp d, Elfin Forest Camp, ca. 2225 m.

Abundances are: C=common, recorded daily in moderate to large numbers (>10 individuals); FC=fairly common, recorded daily in small numbers (<10 individuals); U=uncommon, recorded on one out of three days, occurs in small numbers; R=rare, recorded on one of six days or less often, occurs in small numbers; X=present, not enough information to make a determination of abundance.

[2] See Fitzpatrick and O'Neill 1986

[3] Sight record by N. Krabbe during visit to west slope and crest of Cutucú during April 1984

[4] See Fjeldså and Krabbe 1986

[5] See Schulenberg and Gill 1987

APPENDIX 2

Specimens collected in the Cordillera de Cutucú by L. Gomez between 1937 and 1939[1]

Micrastur buckleyi	2
Geotrygon montana	3
Selenidera reinwardtii	2, 3
Xiphorhynchus ocellatus	3
Philydor erythrocercus	3
Philydor ruficaudatus	3
Herpsilochmus rufimarginatus	3
Myiophobus phoenicomitra	3
Cotinga cayana	2
Pipra erythrocephala	2
Cyanocorax violaceus	3
Dendroica petechia	2
Dendroica fusca	3
Mniotilta varia	2
Setophaga ruticilla	2
Wilsonia canadensis	2
Piranga rubra	2
Sporophila luctuosa	2
Psarocolius decumanus	3

1 Specimen identifications not confirmed by us.
2 Deposited in the British Museum of Nat. History, Tring.
3 Deposited in American Museum of Natural History

Proceedings of The Academy of Natural Sciences of Philadelphia 139: 261-305, 1987

Current Status of the Type Collection (Bacillariophyceae) in the Diatom Herbarium, The Academy of Natural Sciences of Philadelphia

Ronald K. Mahoney and Charles W. Reimer

Department of the Diatom Herbarium, The Academy of Natural Sciences of Philadelphia
19th and the Parkway, Philadelphia, PA 19103

Abstract.— This report presents a current listing of known types and type material present in the Diatom Herbarium (ANSP). The catalogued entries serve as baseline data for an in-depth search for types and type material currently underway. Information presented includes: an alphabetical listing of taxa grouped by genus followed by species, variety and form; author(s) of the taxa; type designation; slide number; date of valid publication; and a number coded literature citation. [Academy of Natural Sciences, Bacillariophyta, diatoms, herbarium, systematics, taxonomy, type collection]

In late 1986, the Diatom Herbarium of The Academy of Natural Sciences (ANSP)* began a new phase of its curating program. The object of this current program is to organize and add to our preliminary inventory of type specimens and type material (National Science Foundation Grant BSR-8518903), thereby establishing a formal type collection.

From a modest beginning about 25 years ago, the herbarium has recorded types in the card catalog as the opportunity arose. These entries have included: a) new taxa described by staff members, b) some earlier types uncovered from the main collection concomitant to other research projects, and c) types sent to the Academy's Diatom Herbarium for deposit by other diatomists. The total number of types cataloged by this procedure is now 1184. Prior to the receipt of current NSF support, no time or funds have been available for determining the extent of our holdings of earlier types.

Information on earlier slides and loose material, variously acquired by the herbarium since about 1860, seldom included special information, or direct reference to newly described species, varieties, or forms. It was not until some years after the type method was incorporated into the International Code of Botanical Nomenclature (Briquet 1935) that diatomists began generally to conform to this provision by specifically designating specimens and/or material as reference points for new taxa. The "*ex post facto*" nature of the ICBN rules requiring designation of types has left our herbarium (as well as many others) with a rich potential of unmarked types from variously curated (by locality, taxon, or author) older herbarium slides and loose material. In our case, the number of slides and material amounts to well over 125,000.

---

* Beginning with Index Herbariorum, Edition 8, (Holmgren 1987), to be identified by the acronym ANSP.

As a prelude to the herbarium search for earlier type material, it was first necessary to re-check and bring together as a computer based inventory the type entries currently listed in the card catalog file. This inventory has now been completed and the results are reported in the list following the introduction and key.

Type designation entries reported as: H (Holotype), L (Lectotype), N (Neotype), or P (Paratype) represent designations as given by the original author(s). The herbarium assumes no resposibility for the legitimacy or validity of these names. There is no intent of introducing new species, new names, or new combinations of any sort in this publication.

Entries marked as I (Isotype Material) are largely interpretations of the herbarium, [i.e. that the material was a part of the original (single) gathering], except in a very few recent cases where the original author(s) clearly has indicated a slide or material as being "Isotype."

Entries marked as I* indicate situations where the original author(s) listed more than one sample with no designation as to which one was the type for the new taxon.

It must be emphasized that this list is a preliminary one. It includes only those types we have been able to curate as explained in the second paragraph. We anticipate a major increase in the listing by the end of the current grant period. At that time we will present a revised listing.

The authors feel that this list of catalogued and presently available types in the Diatom Herbarium (ANSP), with additional information such as accession number, place of original publication and later type designation of earlier taxa, will be of value to those pursuing taxonomic and/or systematic research on diatoms. In any event, it should save a considerable amount of literature searching and correspondence time in locating the whereabouts of particular types.

KEY TO THE DIATOM HERBARIUM (ANSP) CATALOGUE OF TYPE MATERIAL

Information for each type entry is presented in the following order:

1. Specific and varietal epithets (followed by "forma" if necessary) in *italics*. The author(s) of the basionym are given in roman type after the appropriate epithet. Autonyms are included as a part of the epithet in conformation with ICBN Article 26 (Stafleu 1983).

2. Type designation. (expressed as a single capital letter): H = Holotype, L = Lectotype, N = Neotype, P = Paratype, I = Isotype Material, I* = possible isotype material, one of two or more sample listed in the original publication.

3. Slide accession number [in brackets]. In the following lists, a distinction is made between "collection" and "exsiccata." The word "collection" is used when a particular assemblage of slides and/or material is unique. The word "exsiccata" is used to designate a set of slides and/or material representing a duplication of the original set of studied materials. In all cases of the latter condition, such slides are marked as "I" unless a particular slide has been later designated as a type.

a. Slides listed with the following prefixes are housed in the Diatom Herbarium (ANSP), and are catalogued under the given collection or exsiccata:

Boy.	= C.S. Boyer Collection
Cl.&Möll.	= P.T. Cleve & J.D. Möller Exsiccata
Febiger	= C. Febiger Collection
G.C.	= General Collection (ANSP)
H.L.Sm. O	= H.L. Smith Collection (Original)
H.L.S. EX.	= H.L. Smith Exsiccata
Kützing	= F.T. Küzing Exsiccata (Aqua Dulcis Germanicorum)
Rabh. TTO	= L. Rabenhorst Exsiccata (Totius Terrarum Orbis)
Shulze AR	= J. Shulze Arranged Collection

Shulze A = J. Shulze "A" Collection
T&P I = J. Tempère & H. Peragallo Exsiccata Ed. I
T&P II = J. Tempère & H. Peragallo Exsiccata Ed. II
VanHeurck = H. Van Heurck Exsiccata
Wm.Smith = William Smith Exsiccata

b. Slides listed with the following prefixes are housed in herbaria other than the Diatom Herbarium (ANSP). These few entries are added to refer to research work with published citations by staff members of the Diatom Herbarium (ANSP).

Agardh = C. A. Agardh Collection
A.Mayer = A. Mayer Collection
CJElmore = C. J. Elmore Collection
ILL = Iowa Lakeside Laboratory Colletion
J.Grant = J. Grant Collection
PhyUniv. = Phycotheca Universalis Exsiccata
Ward = D. B. Ward Collection

Slides housed in herbaria other than the Diatom Herbarium (ANSP) have a one letter suffix attached to the slide number to indicate their location. These suffixes are:

I = Iowa Lakeside Laboratory
L = Lund University
N = New York Botanical Garden
R = Regensburg

4. Publication date of basionym. In the few cases of name-change entry, the basionym, followed by the year and literature citation number, all enclosed in brackets { }, appears after the first literature citation.

5. Literature citation number for original description, (in parenthesis).

6. Designation of type. In a few cases there is an added entry (in boldface type, **Design.**:) for the later designation of a type. The name of the author who designated the type is given followed by the year of designation and the literature citation number.

7. Transfer of basionym. This is in boldface type (**Tfr.**:) and is followed by the name of the author, date of transfer, and literature citation number.

N.B. Very few entries of C.S. Boyer (a former curator of diatoms, ANSP) are to be found in this list since an in-depth study of his collection for types has never been made. A complete account of Boyer's types will appear shortly in another paper confined to his publications and types.

The authors express thanks to Ms. Su I. Yong and Ms. Margaret Henderson for their assistance with data search and for editorial comments. Technical assistance in manuscript production was provided by Dr. Haydon Rochester and Ms. Robin Davis. Appreciation is expressed to Drs. Ruth Patrick and Robert Ross for careful review of the manuscript. Financial assistance from the National Science Foundation (Grant BSR-8518903) is also gratefully acknowledged.

Briquet, J. 1935. International Rules of Botanical Nomenclature adopted by the International Botanical Congress of Vienna, 1905, and Brussels, 1910, revised by the editorial committee for nomenclature from the report of the subsection of nomenclature. Gustav Fischer, Jena. 151 pp.

Holmgren, P. K. 1987. Index Herbariorum, Edition 8. In press.

Stafleu, F. A. 1983. International Code of Botanical Nomenclature adopted by the Thirteenth International Botanical Congress, Sydney, August, 1981. W. Junk, The Hague/ Boston. 472 pp.

CATALOGUED TYPES AND TYPE MATERIAL

Achnanthes

abundans Manguin in Bourrelly & Manguin var. *abundans*: I*, [G.C. 91506], 1954, (10).
acares Hohn & Hellerman: H, [G.C. 44450], 1963, (60).
alaskana Patrick & Freese: H, [G.C. 8217a], 1961, (119).
alaskana Patrick & Freese: I, [G.C. 8217b], 1961, (119).
aretasii Manguin in Bourrelly & Manguin: I, [G.C. 91506], 1954, (10).
asymbasia Hohn: H, [G.C. 25860a], 1966, (58).
biporoma Hohn & Hellerman: H, [G.C. 44261a], 1963, (60).
biporoma Hohn & Hellerman: I, [G.C. 44261b], 1963, (60).
calcar var. *australis* Playfair: I*, [G.C. 40025a], 1915, (122).
calcar var. *australis* Playfair: I*, [G.C. 40026a], 1915, (122).
calcar var. *pulcherrima* Playfair: I*, [G.C. 40023a], 1915, (122).
chilensis var. *subaequalis* Reimer in Patrick & Reimer: H, [G.C. 4451a], 1966, (120).
chilensis var. *subaequalis* Reimer in Patrick & Reimer: I, [G.C. 4451b], 1966, (120).
chlidanos Hohn & Hellerman: H, [G.C. 44453], 1963, (60).
cincta Andrews: I, [G.C. 63060], 1971, (5).
cocconeioides Riznyk: H, [G.C. 62634], 1973, (149).
confusa Manguin in Bourrelly & Manguin var. *confusa*: I, [G.C. 91506], 1954, (10).
decipiens Reimer: H, [G.C. 44260a], 1966, (143).
decipiens Reimer: I, [G.C. 44260b], 1966, (143).
deflexa var. *alpestris* Lowe & Kociolek: H, [G.C. 53918], 1984, (92).
deflexa Reimer in Patrick & Reimer var. *deflexa*: H, [G.C. 1931], 1966, (120).
detha Hohn & Hellerman: H, [G.C. 44272a], 1963, (60).
detha Hohn & Hellerman: I, [G.C. 44272b], 1963, (60).
germainii Manguin in Bourrelly & Manguin: I, [G.C. 91506], 1954, (10).
grana Hohn & Hellerman: H, [G.C. 44450], 1963, (60).
groenlandica var. *phinneyi* McIntire & Reimer: H, [G.C. 62653], 1974, (97).
groenlandica var. *phinneyi* f. *jaydei* McIntire & Reimer: H, [G.C. 62650], 1974, (97).
harveyi Reimer: H, [G.C. 44254a], 1966, (143).
harveyi Reimer: I, [G.C. 44254b], 1966, (143).
heterostriatoides Hohn: H, [G.C. 25858a], 1966, (58).
jamaicense Podzorski: I, [G.C. 15547], 1985, (125).
kryophiloides Hohn: H, [G.C. 25858a], 1966, (58).
kryophiloides Foged: I, [G.C. 92681], 1964, (39).

Achnanthes (continued)

lacunicola Patrick & Freese: H, [G.C. 8248a], 1961, (119).
lacunicola Patrick & Freese: I, [G.C. 8248b], 1961, (119).
lanceolata var. *abbreviata* Reimer: H, [G.C. 43857a], 1966, (143).
lanceolata var. *apiculata* Patrick: H, [G.C. 2190], 1945, (110).
lanceolata var. *elliptica* Cleve: I, [G.C. 12045], 1891, (21).
lanceolata var. *omissa* Reimer in Patrick & Reimer: H, [G.C. 8526], 1966, (120).
latestriata Riznyk: H, [G.C. 62629], 1973, (149).
lewisiana Patrick: H, [G.C. 2210], 1945, (110).
linearis var. *linearis* f. *curta* H.L. Smith in Boyer: I, [Boy. A-V-4], 1916, (12).
manguinii var. *elliptica* Manguin in Bourrelly & Manguin: I, [G.C. 91506], 1954, (10).
mica Hohn: H, [G.C. 25858a], 1966, (58).
modesta Manguin in Bourrelly & Manguin: I*, [G.C. 91506], 1954, (10).
monela Hohn & Hellerman: H, [G.C. 44914], 1963, (60).
oestrupii var. *parvula* Patrick: H, [G.C. 2209], 1945, (110).
oregonensis Riznyk: H, [G.C. 62634], 1973, (149).
orellana Hohn: H, [G.C. 25862a], 1966, (58).
pelta Hohn & Hellerman: H, [G.C. 44906], 1966, (61).
punctulata Simonsen ex Patrick & Freese: H, [G.C. 8183a], 1966, (119).
punctulata Simonsen ex Patrick & Freese: I, [G.C. 8183b], 1966, (119).
punctulata Simonsen ex Patrick & Freese: I, [G.C. 8183c], 1966, (119).
radiatus Hohn & Hellerman: H, [G.C. 44911], 1966, (61).
recava Hohn & Hellerman: I, [G.C. 44891], 1966, (61).
recava Hohn & Hellerman: H, [G.C. 44891a], 1966, (61).
reimeri Camburn in Camburn, Lowe and Stoneburner: H, [G.C. 53752], 1978, (18).
ricula Hohn & Hellerman: H, [G.C. 44468], 1963, (60).
rupestoides Hohn: H, [G.C. 44476], 1961, (57).
similis McCall: I, [G.C. 11054a], 1933, (96).
similis McCall: I, [G.C. 11054b], 1933, (96).
similis McCall: I, [G.C. 11054c], 1933, (96).
stauroneioides Manguin in Bourrelly & Manguin var. *stauroneioides*: I*, [G.C. 91056], 1954, (10).
stewartii Patrick: H, [G.C. 2194], 1945, (110).
sublaevis var. *crassa* Reimer in Patrick & Reimer: H, [G.C. 44716a], 1966, (120).
subrostrata var. *appalachiana* Camburn & Lowe: H, [G.C. 53753], 1978, (17).
taeniata Grunow in Cleve & Grunow var. *taeniata*: I, [Febiger 4783], 1880, (26).
utukakensis Patrick & Freese: H, [G.C. 8217a], 1961, (119).
utukakensis Patrick & Freese: I, [G.C. 8217b], 1961, (119).
yaquinensis McIntire & Reimer: H, [G.C. 62647], 1974, (97).

Achnanthidium

lanceolatum Brébisson ex Kützing var. *lanceolatum*: I, [Febiger 3119], 1846, (82).
minutum Cleve: I, [G.C. 12045], 1891, (21).

Actinella

punctata Lewis var. *punctata*: I, [Febiger 2372], 1864, (88).

Actinocyclus

sagittulus Villareal in Villareal & Fryxell: I, [G.C. 20318], 1983, (174).

Ambistria

hyalina Lohman & Andrews: I, [G.C. 63058], 1968, (90).
punctata Lohman & Andrews: I, [G.C. 63058], 1968, (90).

Amphipleura

arctica Patrick & Freese: H, [G.C. 8182], 1961, (119).
pellucida (Kützing) Kützing var. *pellucida*: L, [Kützing 83], 1844, (81), {*Frustulia pellucida* Kützing var. *pellucida*, 1833, (80)}, **Tfr.:** Kützing, 1844, (81), **Design.:** Patrick in Patrick & Reimer, 1966, (120).

Amphiprora

alata var. *angustior* McCall: I, [G.C. 11067a], 1933, (96).
alata var. *angustior* McCall: I, [G.C. 11067b], 1933, (96).
incompta Hohn & Hellerman: H, [G.C. 44902], 1966, (61).
robusta McCall: I, [G.C. 11054a], 1933, (96).
robusta McCall: I, [G.C. 11054b], 1933, (96).
robusta McCall: I, [G.C. 11054c], 1933, (96).

Amphora

adumbrata Hohn & Hellerman: H, [G.C. 44912], 1966, (61).
alaskana Patrick & Freese: H, [G.C. 8197a], 1961, (119).
alaskana Patrick & Freese: I, [G.C. 8197b], 1961, (119).
alaskana Patrick & Freese: I, [G.C. 8197c], 1961, (119).
alaskana Patrick & Freese: I, [G.C. 8197d], 1961, (119).
allanta Hohn & Hellerman: H, [G.C. 44890], 1966, (61).
atacamana Patrick: H, [G.C. 26098a], 1961, (114).
atacamana Patrick: I, [G.C. 26098b], 1961, (114).
atacamana Patrick: I, [G.C. 26098c], 1961, (114).
australiensis John: I, [G.C. 40078], 1981, (69).
berggrenii Cleve in Cleve & Möller: I, [Cl.&Möll. 90], 1878, (27).
bicapitata Hohn & Hellerman: H, [G.C. 44892], 1966, (61).
birnirkiana Patrick & Freese: I, [G.C. 8214a], 1961, (119).
birnirkiana Patrick & Freese: H, [G.C. 8214b], 1961, (119).

Amphora (continued)

birugula Hohn: H, [G.C. 44483], 1961, (57).
birugula Hohn: I, [G.C. 44484], 1961, (57).
blaingraysia Selva: H, [G.C. 63092], 1981, (155).
boliviana Patrick: H, [G.C. 26098a], 1961, (114).
boliviana Patrick: I, [G.C. 26098b], 1961, (114).
boliviana Patrick: I, [G.C. 26098c], 1961, (114).
bullatoides Hohn & Hellerman: H, [G.C. 44469], 1963, (60).
carvajaliana Patrick: H, [G.C. 26100a], 1961, (114).
coffeiformis (Agardh) Kützing var. *coffeiformis*: I, [G.C. 13668], 1844, (81), {*Frustulia coffeaeformis* Agardh var. *coffeaeformis*, 1827, (1)}, **Tfr.:** Kützing, 1844, (81).
coffeiformis (Agardh) Kützing var. *coffeiformis*: L, [Agardh 4600 L], 1844, (81), {*Frustulia coffeaeformis* Agardh var. *coffeaeformis*, 1827, (1)}, **Tfr.:** Kützing, 1844, (81), **Design.:** Reimer in Patrick & Reimer, 1975, (121).
delapunctata Hohn & Hellerman: H, [G.C. 44906], 1966, (61).
doddii Selva: H, [G.C. 63093], 1981, (155).
katii Selva: H, [G.C. 63094], 1981, (155).
lagerheimii var. *minuta* Playfair: I, [G.C. 40021a], 1916, (123).
menisca Hohn & Hellerman: H, [G.C. 44496], 1963, (60).
multigramma Hohn & Hellerman: H, [G.C. 44906], 1966, (61).
nuwukiana var. *arctica* Patrick & Freese: H, [G.C. 8154a], 1961, (119).
nuwukiana var. *arctica* Patrick & Freese: I, [G.C. 8154b], 1961, (119).
nuwukiana Patrick & Freese var. *nuwukiana*: H, [G.C. 8213a], 1961, (119).
ovalis var. *barrowiana* Patrick & Freese: H, [G.C. 8183a], 1961, (119).
ovalis var. *barrowiana* Patrick & Freese: I, [G.C. 8183b], 1961, (119).
ovalis var. *barrowiana* Patrick & Freese: I, [G.C. 8183c], 1961, (119).
paulii Patrick: H, [G.C. 26622], 1970, (117).
pleniluna Hohn & Hellerman: H, [G.C. 44902], 1966, (61).
punctata Andrews: I, [G.C. 63060], 1971, (5).
robertsonii Podzorski: I, [G.C. 15545], 1985, (125).
roettgeri Lee & Reimer: H, [G.C. 40096], 1984, (87).
sabiniana Reimer in Patrick & Reimer: H, [G.C. 8027], 1975, (121).
salsa Patrick & Freese: H, [G.C. 8211], 1961, (119).
spartinetensis Sullivan & Reimer: H, [G.C. 53122], 1975, (163).
staurohyalina Podzorski & Håkansson: I, [G.C. 90608], 1987, (126).
stroppiana Selva: H, [G.C. 63092], 1981, (155).
subhyalina Podzorski & Håkansson: I, [G.C. 90608], 1987, (126).
testudinata Hohn & Hellerman: H, [G.C. 44902], 1966, (61).
veneta var. *grossestriata* Playfair: I*, [G.C. 40022a], 1915, (122).
veneta var. *grossestriata* Playfair: I*, [G.C. 40023a], 1915, (122).
veneta var. *grossestriata* Playfair: I*, [G.C. 40025a], 1915, (122).
veneta var. *grossestriata* Playfair: I*, [G.C. 40026a], 1915, (122).

Anaulus

ovalis Lohman & Andrews: I, [G.C. 63058], 1968, (90).

Anomoeoneis

fogedii Reimer: H, [ILL S.P.-33 I], 1982, (145).
follis var. *fossilis* Reimer: H, [G.C. 45101], 1961, (141).
follis var. *hannae* Reimer: H, [Boy. 818], 1961, (141).
follis var. *hannae* Reimer: P, [Boy. 818], 1961, (141).
irawane Podzorski & Håkansson: I, [G.C. 90607], 1987, (126).
sphaerophora var. *intermedia* McCall: I, [G.C. 11055], 1933, (96).
undulata Lohman & Andrews: I, [G.C. 63058], 1968, (90).

Arcocellulus

cornucervis Hasle, von Stosch & Syvertsen: I, [G.C. 95354], 1983, (51).
mammifer Hasle, von Stosch & Syvertsen: I, [G.C. 95355], 1983, (51).

Asterionella

notata var. *recticostata* Koerner: I, [G.C. 35613], 1970, (76).

Aulacodiscus

concentricus (Mann) Boyer: I, [G.C. 5125], 1927, (15), {*Tripodiscus concentricus* Mann, 1907, (94)}, **Tfr.**: Boyer, 1927, (15).

Bellerochea

horologicalis von Stosch var. *horologicalis*: I, [G.C. 53856a], 1980, (175).
horologicalis von Stosch var. *horologicalis*: I, [G.C. 53856b], 1980, (175).
horologicalis var. *recta* von Stosch: I, [G.C. 40109], 1987, (177).
yucatanensis von Stosch: I, [G.C. 30876a], 1980, (175).
yucatanensis von Stosch: I, [G.C. 30876b], 1980, (175).

Bennettella

wheeleri (Hart) Holmes: I, [G.C. 91178], 1985, (62), {*Cocconeis wheeleri* Hart, 1935, (49)}, **Tfr.**: Holmes, 1985, (62).

Biddulphia

inusitata Hohn & Hellerman: H, [G.C. 44907], 1966, (61).

Caloneis

barrowiana Patrick & Freese: I, [G.C. 8244a], 1961, (119).
barrowiana Patrick & Freese: H, [G.C. 8244b], 1961, (119).
glaberrima Østrup: I*, [G.C. 12571], 1910, (103).
ladogensis var. *densistriata* Østrup: I*, [G.C. 12568], 1910, (103).

Caloneis (continued)

latiuscula var. *reimeri* Czarnecki & Blinn: H, [G.C. 63427a], 1979, (31).
latiuscula var. *reimeri* Czarnecki & Blinn: I, [G.C. 63427b], 1979, (31).
latiuscula var. *reimeri* Czarnecki & Blinn: I, [G.C. 63427c], 1979, (31).
latiuscula var. *reimeri* Czarnecki & Blinn: I, [G.C. 63427d], 1979, (31).
lewisii Patrick var. *lewisii*: H, [G.C. 2018], 1945, (110).
marnieri Manguin in Bourrelly & Manguin: I*, [G.C. 91506], 1954, (10).
oregonica var. *quadrilineata* (Grunow ex Cleve) Patrick in Patrick & Reimer: L, [Cl.&Möll. 204], 1966, (120), {*Caloneis formosa* var. *quadrilineata* Grunow ex Cleve, 1894, (24)}, **Tfr.:** & **Design.:** Patrick in Patrick & Reimer, 1966, (120).
salebrastriata Hohn: H, [G.C. 44484], 1961, (57).

Caponea

caribbea Podzorski: I, [G.C. 15546], 1984, (124).

Chaetoceros

elmorei Boyer: I, [Boy. C-I-2], 1914, (11).
elmorei Boyer: I, [Boy. X-V-14], 1914, (11).
elmorei Boyer: I, [G.C. 5028], 1914, (11).
elmorei Boyer: I, [G.C. 8436], 1914, (11).
elmorei Boyer: I, [G.C. 8437], 1914, (11).

Cocconeis

amydrofilum Riznyk: H, [G.C. 62632], 1973, (149).
arenicola Riznyk: H, [G.C. 62634], 1973, (149).
californica var. *lengana* Rivera in Rivera, Parra and Gonzelez: I, [G.C. 26647], 1973, (148).
delalineata Hohn: H, [G.C. 44474], 1961, (57).
delapunctata Hohn: H, [G.C. 44489], 1961, (57).
fluviatilis Wallace: I, [G.C. 3872a], 1960, (178).
fluviatilis Wallace: H, [G.C. 3872b], 1960, (178).
inusitatus Hohn: H, [G.C. 44474], 1961, (57).
nugalas Hohn & Hellerman: H, [G.C. 44902], 1966, (61).
patrickiae Reimer: H, [G.C. 45669], 1961, (142).
woodii Reyes-Vasquez: H, [G.C. 48281], 1970, (147).

Colletonema

bullosa Fiorini-Mazzanti var. *bullosa*: I, [G.C. 10540], 1856, (35).
bullosa Fiorini-Mazzanti var. *bullosa*: I, [G.C. 10541], 1856, (35).

Coscinodiscus

bulla Hohn & Hellerman: H, [G.C. 44899], 1966, (61).
lacustris var. *denticulatus* Playfair: I, [G.C. 40026a], 1915, (122).
lacustris var. *tympaniformis* Playfair: I, [G.C. 40026a], 1915, (122).
lewisianus var. *hillabyanus* Boyer: I, [G.C. 15439], 1922, (14).
litos Hohn & Hellerman: H, [G.C. 44907], 1966, (61).
subtilis var. *radiatus* Hohn: I, [G.C. 4149a], 1952, (56).
subtilis var. *radiatus* Hohn: I, [G.C. 4149b], 1952, (56).

Cyclostephanos

fenestratus Theriot & Kociolek: H, [G.C. 64151a], 1986, (170).
fenestratus Theriot & Kociolek: I, [G.C. 64151b], 1986, (170).
undatus Theriot & Kociolek: H, [G.C. 64152a], 1986, (170).
undatus Theriot & Kociolek: I, [G.C. 64152b], 1986, (170).

Cyclotella

aliquantula Hohn & Hellerman: H, [G.C. 8024], 1963, (89).
andina Theriot, Carney & Richerson: H, [G.C. 26720], 1985, (169).
facetai Hohn & Hellerman: H, [G.C. 8102], 1963, (60).
meneghiniana var. *brevistriata* Playfair: I, [G.C. 40027a], 1915, (122).
meneghiniana var. *convexa* Playfair: I*, [G.C. 40022a], 1915, (122).
meneghiniana var. *convexa* Playfair: I*, [G.C. 40023a], 1915, (122).
meneghiniana var. *convexa* Playfair: I*, [G.C. 40024a], 1915, (122).
meneghiniana var. *convexa* Playfair: I*, [G.C. 40025a], 1915, (122).
meneghiniana var. *fluviatilis* Playfair: I*, [G.C. 40027a], 1915, (122).
meneghiniana Kützing var. *meneghiniana*: I, [G.C. 13664], 1844, (81).
meneghiniana var. *quadrata* Playfair: I*, [G.C. 40022a], 1915, (122).
meneghiniana var. *quadrata* Playfair: I*, [G.C. 40023a], 1915, (122).
meneghiniana var. *quadrata* Playfair: I*, [G.C. 40027a], 1915, (122).
pseudostelligera var. *pseudostelligera* f. *parva* Czarnecki & Blinn: H, [G.C. 63428a], 1979, (31).
pseudostelligera var. *pseudostelligera* f. *parva* Czarnecki & Blinn: I, [G.C. 63428b], 1979, (31).
pseudostelligera var. *pseudostelligera* f. *parva* Czarnecki & Blinn: I, [G.C. 63428c], 1979, (31).
pseudostelligera var. *pseudostelligera* f. *parva* Czarnecki & Blinn: I, [G.C. 63428d], 1979, (31).
seratula Hohn & Hellerman: H, [G.C. 44453], 1963, (60).
shanxiensis Xie & Qi: I, [G.C. 35754a], 1984, (181).
shanxiensis Xie & Qi: I, [G.C. 35754b], 1984, (181).
shanxiensis Xie & Qi: I, [G.C. 35754c], 1984, (181).
shanxiensis Xie & Qi: I, [G.C. 35754d], 1984, (181).
shanxiensis Xie & Qi: I, [G.C. 35754e], 1984, (181).
shanxiensis Xie & Qi: I, [G.C. 35754f], 1984, (181).
shanxiensis Xie & Qi: I, [G.C. 35754g], 1984, (181).
shanxiensis Xie & Qi: I, [G.C. 35754h], 1984, (181).

Cyclotella (continued)

shanxiensis Xie & Qi: I, [G.C. 35754i], 1984, (181).
shanxiensis Xie & Qi: I, [G.C. 35754j], 1984, (181).
shanxiensis Xie & Qi: I, [G.C. 35754k], 1984, (181).
shanxiensis Xie & Qi: I, [G.C. 35754l], 1984, (181).
shanxiensis Xie & Qi: I, [G.C. 35754m], 1984, (181).
shanxiensis Xie & Qi: I, [G.C. 35754n], 1984, (181).
shanxiensis Xie & Qi: I, [G.C. 35754o], 1984, (181).
shanxiensis Xie & Qi: I, [G.C. 35754p], 1984, (181).
shanxiensis Xie & Qi: I, [G.C. 35754q], 1984, (181).
shanxiensis Xie & Qi: I, [G.C. 35754r], 1984, (181).

Cymbella

acuta (A. Schmidt) Cleve var. *acuta*: L, [Cl.&Möll. 321], 1894, (24), {*Cymbella americana* var. *acuta* A. Schmidt, 1881, (153), **Tfr.**: Cleve, 1894, (24), **Design.**: Reimer in Patrick & Reimer, 1975, (121).
alaskana Patrick & Freese: H, [G.C. 8223a], 1961, (119).
alaskana Patrick & Freese: I, [G.C. 8223b], 1961, (119).
antogaryana Selva: H, [G.C. 63095], 1981, (155).
aspera var. *gigas* McCall: I, [G.C. 11056a], 1933, (96).
aspera var. *gigas* McCall: I, [G.C. 11056b], 1933, (96).
cassidula Hohn & Hellerman: H, [G.C. 44907], 1966, (61).
cesatii var. *linearis* Reimer: H, [G.C. 45669], 1961, (142).
cesatii var. *schreinfrankii* Selva: H, [G.C. 63096], 1981, (155).
clausii Van Landingham: I, [G.C. 49722], 1966, (173).
delicatissima var. *beagleana* Patrick: H, [G.C. 26621a], 1970, (117).
delicatula var. *intermedia* McCall: H, [G.C. 11057], 1933, (96).
fluminea Patrick & Freese: I, [G.C. 8197a], 1961, (119).
fluminea Patrick & Freese: I, [G.C. 8197b], 1961, (119).
fluminea Patrick & Freese: H, [G.C. 8197c], 1961, (119).
fluminea Patrick & Freese: I, [G.C. 8197d], 1961, (119).
gibba J.W. Bailey in L.W. Bailey: L, [H.L.S.O A-92], 1861, (9), **Design.**: Reimer in Patrick & Reimer, 1975, (121).
hauckii Van Heurck in Hauck & Richter var. *hauckii*: I, [G.C. 13709], 1887, (52), **Design.**: Reimer in Patrick & Reimer, 1975, (121).
hauckii Van Heurck in Hauck & Richter var. *hauckii*: L, [PhyUniv 147 L], 1887, (52).
lacustris var. *australis* Manguin in Bourrelly & Manguin: I, [G.C. 91506], 1954, (10).
laevis Naegeli in Kützing var. *laevis*: L, [G.C. 13667], 1849, (83), **Design.**: Reimer in Patrick & Reimer, 1975, (121).
laterostrata var. *alaskana* Patrick & Freese: H, [G.C. 8223a], 1961, (119).

Cymbella (continued)

laterostrata var. *alaskana* Patrick & Freese: I, [G.C. 8223b], 1961, (119).
lineolatea Patrick: H, [G.C. 25739], 1944, (109).
lunata Wm. Smith in Greville var. *lunata*: L, [Wm.Smith 290], 1855, (46), **Design.:** Reimer in Patrick & Reimer, 1975, (121).
marcinia Selva: H, [G.C. 63096], 1981, (155).
menisculis Hohn: H, [G.C. 25858a], 1966, (58).
microcephala var. *crassa* Reimer in Patrick & Reimer: H, [G.C. 6590a], 1975, (121).
microcephala var. *crassa* Reimer in Patrick & Reimer: I, [G.C. 6590b], 1975, (121).
minuta var. *silesiaca* (Bleisch ex Rabenhorst) Reimer in Patrick & Reimer: L, [G.C. 11486], 1975, (121), {*Cymbella silesiaca* Bleisch ex Rabenhorst var. *silesiaca*, 1865, (134)}, **Tfr.:** & **Design.:** Reimer in Patrick & Reimer, 1975, (121).
muelleri var. *muelleri* f. *ventricosa* (Tempère & Peragallo) Reimer in Patrick & Reimer: L, [T&P I 524], 1975, (121), {*Encyonema turgidum* var. *ventricosa* Tempère & Peragallo, 1895, (166)}, **Tfr.:** & **Design.:** Reimer in Patrick & Reimer, 1975, (121).
pediculus Kützing: I*, [G.C. 13707], 1844, (81).
pediculus Kützing: I*, [G.C. 13708], 1844, (81).
proxima var. *gravida* Reimer in Patrick & Reimer: H, [G.C. 1909], 1975, (121).
proxima Reimer in Patrick & Reimer var. *proxima*: H, [VanHeurck 24], 1975, (121).
semigibbosa Patrick & Freese: H, [G.C. 8221], 1961, (119).
similis Patrick var. *similis*: H, [G.C. 1726], 1943, (107).
tasmaniensis var. *alaskana* Patrick & Freese: H, [G.C. 8217a], 1961, (119).
tasmaniensis var. *alaskana* Patrick & Freese: I, [G.C. 8217b], 1961, (119).
turgida var. *barrowiana* Patrick & Freese: I, [G.C. 8283a], 1961, (119).
turgida var. *barrowiana* Patrick & Freese: H, [G.C. 8283b], 1961, (119).
turgida Gregory var. *turgida*: I, [Febiger 3469], 1856, (45).
vestigiana Patrick & Freese: H, [G.C. 8298a], 1961, (119).
vestigiana Patrick & Freese: I, [G.C. 8298b], 1961, (119).

Desmogonium

femoriforme Patrick: H, [G.C. 25415a], 1940, (105).
rabenhorstianum var. *elongatum* Patrick: H, [G.C. 25416a], 1940, (105).

Dextradonator

jeremianus Ross & Sims: H, [ShulzeAR 2668], 1980, (150).

Diatoma

anceps var. *linearis* M. Peragallo: L, [T&P II 104], 1908, (167),
Design.: Patrick in Patrick & Reimer, 1966, (120).

Diatomella

hustedtii Manguin in Bourrelly & Manguin: I*, [G.C. 91506], 1954, (10).

Dimerogramma

brandywinensis Patrick: H, [G.C. 2296], 1944, (108).

Diploneis

boldtiana var. *australica* Playfair: I*, [G.C. 40025a], 1915, (122).
boldtiana var. *australica* Playfair: I*, [G.C. 40027a], 1915, (122).
boldtiana var. *ovalis* Playfair: I*, [G.C. 40025a], 1915, (122).
boldtiana var. *ovalis* Playfair: I*, [G.C. 40027a], 1915, (122).
hormopunctata Hohn & Hellerman: H, [G.C. 8099a], 1966, (61).
hormopunctata Hohn & Hellerman: I, [G.C. 8099b], 1966, (61).
insolitus Hohn & Hellerman: H, [G.C. 44890], 1966, (61).
nitescens var. *candida* McCall: I, [G.C. 11067], 1933, (96).
nitescens var. *candida* McCall: I, [G.C. 11067a], 1933, (96).
ovalis var. *oblongella* f. *gibbosa* McCall: I, [G.C. 11056a], 1933, (96).
ovalis var. *oblongella* f. *gibbosa* McCall: I, [G.C. 11056b], 1933, (96).

Ditylum

buchananii von Stosch: I, [G.C. 40108], 1987, (177).

Epipellis

oiketis Holmes: I, [G.C. 20337], 1985, (62).

Epithemia

gibberula var. *perpusilla* Playfair: I, [G.C. 40027b], 1915, (122).
hyndmanii var. *capitata* M. Peragallo: L, [T&P II 366], 1910, (168),
Design.: Patrick in Patrick & Reimer, 1975, (121).
irregularis Andrews: I, [G.C. 53732], 1966, (3).
kurzeana Rabenhorst: I, [Rabh.TTO 27], 1871, (135).
truncata var. *debilis* M. Peragallo: L, [T&P II 366], 1910, (168),
Design.: Patrick in Patrick & Reimer, 1975, (121).
truncata M. Peragallo var. *truncata*: L, [T&P II 366], 1910, (168),
Design.: Patrick in Patrick & Reimer, 1975, (121).

Eunotia

aduncus Hohn & Hellerman: H, [G.C. 44453], 1963, (60).
attenuata Patrick: H, [G.C. 25419a], 1940, (105).
bilii Lowe & Kociolek: H, [G.C. 53917], 1984, (92).
brevis Patrick: H, [G.C. 25421a], 1940, (105).

Eunotia (continued)

callosa Patrick: H, [G.C. 25420a], 1940, (105).
carolina Patrick: H, [G.C. 44254a], 1958, (111).
carolina Patrick: I, [G.C. 44254b], 1958, (111).
catillifera Morrow in Morrow, Deason and Clayton: H, [G.C. 53770], 1981, (100).
collinsii Kalinsky: H, [G.C. 53901], 1984, (72).
cordillera Hohn & Hellerman: H, [G.C. 44450], 1963, (60).
densistriata Hohn: H, [G.C. 25861a], 1966, (58).
fallax var. *gracillima* Krasske: I, [G.C. 10637a], 1929, (78).
fallax var. *gracillima* Krasske: I, [G.C. 10637b], 1929, (78).
fallax var. *gracillima* Krasske: I, [G.C. 10637c], 1929, (78).
fallax var. *gracillima* Krasske: I, [G.C. 19637d], 1929, (78).
formica var. *richmondiae* Playfair: I*, [G.C. 40022a], 1915, (122).
formica var. *richmondiae* Playfair: I*, [G.C. 40024a], 1915, (122).
formica var. *richmondiae* Playfair: I*, [G.C. 40026a], 1915, (122).
glebula Hohn: H, [G.C. 25862a], 1966, (58).
hexaglyphus Ehrenberg: N, [H.L.Sm.EX 160], 1854, (34), **Design.:** Patrick, 1958, (111).
indica Grunow var. *indica*: I, [G.C. 90503], 1865, (47).
microcephala Krasske ex Hustedt var. *microcephala*: I*, [G.C. 10634a], 1932, (65).
microcephala Krasske ex Hustedt var. *microcephala*: I*, [G.C. 10634b], 1932, (65).
microcephala Krasske ex Hustedt var. *microcephala*: I*, [G.C. 10634c], 1932, (65).
microcephala Krasske ex Hustedt var. *microcephala*: I*, [G.C. 10634d], 1932, (65).
microcephala Krasske ex Hustedt var. *microcephala*: I*, [G.C. 12949], 1932, (65).
monodon var. *major* f. *elongata* Manguin in Bourrelly & Manguin: I*, [G.C. 91506], 1954, (10).
nivalis Hohn & Hellerman: H, [G.C. 44453], 1963, (60).
obesa var. *wardii* Patrick: H, [Ward C-7-17 N], 1958, (111).
occulata Patrick & Freese: H, [G.C. 8195], 1961, (119).
quaternaria Ehrenberg: N, [T&P I 303], 1843, (33), **Design.:** Patrick, 1958, (111).
serra var. *diadema* Ehrenberg: N, [VanHeurck 274], 1837, (32), **Design.:** Patrick, 1958, (111).
serra Ehrenberg var. *serra*: N, [VanHeurck 274], 1837, (32), **Design.:** Patrick, 1958, (111).
torula Hohn: H, [G.C. 44474], 1961, (57).
trinacria var. *undulata* Hustedt: I*, [G.C. 10636a], 1930, (63).
trinacria var. *undulata* Hustedt: I*, [G.C. 10636b], 1930, (63).
trinacria var. *undulata* Hustedt: I*, [G.C. 10636c], 1930, (63).
trinacria var. *undulata* Hustedt: I*, [G.C. 10636d], 1930, (63).

Eunotia (continued)

undata Patrick: H, [G.C. 25120a], 1940, (105).
undata Patrick: I, [G.C. 25121a], 1940, (105).
undata Patrick; I, [G.C. 25256], 1940, (105).
vanheurckii Patrick var. *vanheurckii*: N?, [VanHeurck 274], 1958, (111).
ventriosa Patrick: I, [G.C. 25410], 1940, (105).
ventriosa Patrick: I, [G.C. 25411], 1940, (105).
ventriosa Patrick: I, [G.C. 25414a], 1940, (105).
ventriosa Patrick: H, [G.C. 25418a], 1940, (105).
zasuminensis var. *minor* Kalinsky: H, [G.C. 53902], 1984, (72).

Extubocellus

cribriger Hasle, von Stosch & Syvertsen: I, [G.C. 95353], 1983, (51).

Falcatella

zelleri Rabenhorst: I, [G.C. 10597], 1850, (127).

Florella

portoricensis Navarro: I, [G.C. 75001], 1982, (102).

Fragilaria

alpestris Krasske in Hustedt: I*, [G.C. 12950], 1931, (64).
alpestris Krasske in Hustedt: I*, [G.C. 10635a], 1931, (64).
alpestris Krasske in Hustedt: I*, [G.C. 10635b], 1931, (64).
alpestris Krasske in Hustedt: I*, [G.C. 10635c], 1931, (64).
alpestris Krasske in Hustedt: I*, [G.C. 10635d], 1931, (64).
brevistriata var. *turgida* McCall: I, [G.C. 11064a], 1933, (96).
brevistriata var. *turgida* McCall: I, [G.C. 11064b], 1933, (96).
curvistriata Lohman & Andrews: I, [G.C. 63058], 1968, (90).
denticulata Lohman & Andrews: I, [G.C. 63058], 1968, (90).
dibolos Hohn & Hellerman: H, [G.C. 44458], 1963, (60).
glebula Hohn & Hellerman: H, [G.C. 44467], 1963, (60).
gnathastoma Hohn: H, [G.C. 44489], 1961, (57).
interstincta Hohn & Hellerman var. *interstincta*: H, [G.C. 44469], 1963, (60).
laevissima Østrup var. *laevissima*: I, [G.C. 12569], 1910, (103).
pellucida Lohman & Andrews: I, [G.C. 63058], 1968, (90).
pelta Hohn & Hellerman: H, [G.C. 44890], 1966, (61).
punctata John: H, [G.C. 40076], 1981, (68).
rhodana Hohn & Hellerman: H, [G.C. 44471], 1963, (60).
shiloi Lee, Reimer & McEnery: H, [G.C. 38063], 1980, (86).
silendum Hohn & Hellerman: H, [G.C. 8035], 1966, (61).
sinuata M. Peragallo in Tempère & Peragallo: L, [T&P II 366], 1910, (168), **Design.**: Patrick in Patrick & Reimer, 1966, (120).
spinulosa Patrick: H, [G.C. 25417], 1940, (105).

Fragilaria (continued)

sublika Hohn & Hellerman: H, [G.C. 44453], 1963, (60).
vaucheriae var. *tenuis* Manguin in Bourrelly & Manguin: I*, [G.C. 91506], 1954, (10).
vaucheriae var. *vaucheriae* f. *contorta* Lowe: I, [G.C. 52649], 1972, (91).
virescens var. *nipha* Hohn & Hellerman: H, [G.C. 44453], 1963, (60).
virescens var. *torus* Hohn & Hellerman: H, [G.C. 44902], 1966, (61).

Frustulia

adnata Kützing: I, [G.C. 13705], 1833, (80).
isabelae Patrick: H, [G.C. 26620a], 1970, (117).
isabelae Patrick: I, [G.C. 26620b], 1970, (117).
isabelae Patrick: I, [G.C. 26620c], 1970, (117).
operculata Agardh: I, [G.C. 13711], 1827, (1).
operculata Agardh: I, [G.C. 13712], 1827, (1).
regula Hohn & Hellerman: H, [G.C. 44908], 1966, (61).
ventricosa Agardh: I, [G.C. 13711], 1827, (1).
ventricosa Agardh: I, [G.C. 13712], 1827, (1).

Gomphoneis

eriense var. *apiculata* Stoermer in Reimer: H, [ILL L-2-12 I], 1982, (145).
linearis Kociolek & Stoermer: H, [G.C. 64162], 1986, (75).
trullata Kociolek & Stoermer: H, [G.C. 64161], 1986, (75).

Gomphonema

alaskana Patrick & Freese: H, [G.C. 8226a], 1961, (119).
alaskana Patrick & Freese: I, [G.C. 8226b], 1961, (119).
apuncto Wallace: I, [G.C. 4242a], 1960, (178).
apuncto Wallace: H, [G.C. 4242b], 1960, (178).
augur var. *angulatum* Playfair: I*, [G.C. 40022a], 1915, (122).
augur var. *angulatum* Playfair: I*, [G.C. 40023a], 1915, (122).
augur var. *angulatum* Playfair: I*, [G.C. 40024a], 1915, (122).
augur var. *angulatum* Playfair: I*, [G.C. 40025a], 1915, (122).
augur var. *rotundatum* Playfair: I*, [G.C. 40022a], 1915, (122).
augur var. *rotundatum* Playfair: I*, [G.C. 40023a], 1915, (122).
augur var. *rotundatum* Playfair: I*, [G.C. 40024a], 1915, (122).
augur var. *rotundatum* Playfair: I*, [G.C. 40025a], 1915, (122).
barrowiana Patrick & Freese: I, [G.C. 8242a], 1961, (119).
barrowiana Patrick & Freese: H, [G.C. 8242b], 1961, (119).
cantalicum Brun & Héribaud in Héribaud var. *cantalicum*: I, [G.C. 13305a], 1893, (54).
cantalicum Brun & Héribaud in Héribaud var. *cantalicum*: I, [G.C. 13305b], 1893, (54).

Gomphonema (continued)

cantalicum var. *costalonga* Brun & Héribaud in Héribaud: I, [G.C. 13305a], 1893, (54).
cantalicum var. *costalonga* Brun & Héribaud in Héribaud: I, [G.C. 13305b], 1893, (54).
cholnokyites Van Landingham: H, [G.C. 8519], 1964, (172).
christenseni Lowe & Kociolek: H, [G.C. 53920], 1984, (92).
citera Hohn & Hellerman: H, [G.C. 44458], 1963, (60).
consector Hohn & Hellerman: H, [G.C. 44458], 1963, (60).
constrictum var. *australe* Playfair: I*, [G.C. 40027a], 1915, (122).
cumrhis Hohn & Hellerman: H, [G.C. 44458], 1963, (60).
ellipticum Patrick: H, [G.C. 25733], 1944, (109).
evexus Hohn: H, [G.C. 25865a], 1966, (58).
freesei Lowe & Kociolek: H, [G.C. 53921], 1984, (92).
gibba Wallace: H, [G.C. 4356a], 1960, (178).
gibba Wallace: I, [G.C. 4356b], 1960, (178).
instablis Hohn & Hellerman: H, [Ward F-188-1 N], 1963, (60).
invisitata Hohn & Hellerman: H, [G.C. 44452], 1963, (60).
kerguelenensis Manguin in Bourrelly & Manguin var. *kerguelenensis*: I*, [G.C. 91506], 1954, (10).
lacunicola Patrick & Freese: I, [G.C. 8241a], 1961, (119).
lacunicola Patrick & Freese: H, [G.C. 8241b], 1961, (119).
lacunicola Patrick & Freese: I, [G.C. 8241c], 1961, (119).
lanceolatum Agardh var. *lanceolatum*: I, [G.C. 13671], 1830, (2).
lanceolatum Agardh var. *lanceolatum*: I, [G.C. 13706], 1830, (2).
louisiananum Kalinsky: H, [G.C. 53900], 1984, (72).
malista Hohn & Hellerman: H, [G.C. 44452], 1963, (60).
mehleri Camburn in Camburn, Lowe and Stoneburner: H, [G.C. 53754], 1978, (18).
montezumense Czarnecki & Blinn: H, [G.C. 63426a], 1979, (31).
montezumense Czarnecki & Blinn: I, [G.C. 63426b], 1979, (31).
montezumense Czarnecki & Blinn: I, [G.C. 63426c], 1979, (31).
montezumense Czarnecki & Blinn: I, [G.C. 63426d], 1979, (31).
novacula Hohn & Hellerman: H, [G.C. 44453], 1963, (60).
olivaceiodes var. *hutchinsoniana* Patrick: H, [G.C. 51581], 1971, (118).
septum Moghadam: H, [G.C. 62242], 1969, (99).
simus Hohn & Hellerman: H, [G.C. 44468], 1963, (60).
sparsistriatum var. *sparsistriatum* f. *maculatum* Camburn in Camburn, Lowe and Stoneburner: H, [G.C. 53755], 1978, (18).
stiria Hohn & Hellerman: H, [G.C. 44452], 1963, (60).
tackei var. *brevistriatum* Camburn in Camburn, Lowe and Stoneburner: H, [G.C. 53756], 1978, (18).
turris var. *lineatum* Patrick: H, [G.C. 25729], 1944, (109).

Gomphonitzschia

agma Hohn & Hellerman: H, [G.C. 6653a], 1966, (61).

Gomphonitzschia (continued)

agma Hohn & Hellerman: I, [G.C. 6653b], 1966, (61).

Gyrosigma

attenuatum var. *gigas* McCall: I, [G.C. 11062a], 1933, (96).
attenuatum var. *gigas* McCall: I, [G.C. 11062b], 1933, (96).
distortum var. *undulatum* McCall: I*, [G.C. 11054a], 1933, (96).
distortum var. *undulatum* McCall: I*, [G.C. 11054b], 1933, (96).
distortum var. *undulatum* McCall: I*, [G.C. 11054c], 1933, (96).
distortum var. *undulatum* McCall: I*, [G.C. 11058], 1933, (96).
incompta Hohn & Hellerman: H, [G.C. 44909], 1966, (61).
pallidum Riznyk: H, [G.C. 62630], 1973, (149).
terryanum var. *terryanum* f. *fontanum* Reimer in Patrick & Reimer: H, [G.C. 2861], 1966, (120).

Hantzschia

recta Andrews: I, [G.C. 63060], 1971, (5).

Haslea

gigantea var. *tenuis* von Stosch: I, [G.C. 40100], 1985, (176).

Hyalodiscus

lentiginosus John: H, [G.C. 40064], 1982, (71).

Leyanella

arenaria Hasle, von Stosch & Syvertsen: I, [G.C. 95356], 1983, (51).

Lithodesmioides

minutum von Stosch: I, [G.C. 40107], 1987, (177).
polymorphum von Stosch: I, [G.C. 40106], 1987, (177).

Lithodesmium

duckerae von Stosch: I, [G.C. 40105], 1987, (177).

Mastogloia

canalicula McCall: I*, [G.C. 11060a], 1933, (96).
canalicula McCall: I*, [G.C. 11060b], 1933, (96).
corsicana Grunow in Cleve & Möller var. *corsicana*: I, [Cl.&Möll. 153], 1878, (28).
corsicana var. *johnsonii* Yohn & Gibson: I, [G.C. 15409], 1981, (182).
drouetiana Patrick: H, [G.C. 26620a], 1970, (117).
drouetiana Patrick: I, [G.C. 26620b], 1970, (117).
drouetiana Patrick: I, [G.C. 26620c], 1970, (117).
elegans Lewis: I, [Febiger 2802], 1865, (89).
guatemalensis Patrick: H, [G.C. 30657], 1966, (115).
halophila John: H, [G.C. 40089], 1980, (67).

Mastogloia (continued)

paradoxa Grunow in Cleve & Möller var. *paradoxa*: I, [Cl.&Möll. 153], 1878, (28).
pseudolacrimata Yohn & Gibson: I, [G.C. 15411], 1982, (183).
pseudolatecostata Yohn & Gibson: I, [G.C.15411], 1982, (183).
reimeri John: H, [G.C. 40088], 1980, (67).
rimosa Cleve: I, [Boy. B-VI-20], 1893, (23).
stephensiana Yohn & Gibson: I, [G.C. 15410], 1982, (183).

Melosira

accinctus Hohn & Hellerman: H, [G.C. 44450], 1963, (60).
distans var. *nivaloides* Camburn in Camburn & Kingston: H, [G.C. 54241], 1986, (16).
herzogii var. *minor* Hohn: H, [G.C. 25862a], 1966, (58).
inordinata Lohman & Andrews: I, [G.C. 63058], 1968, (90).
interrupta Lohman & Andrews: I, [G.C. 63058], 1968, (90).
italica var. *multistriata* Patrick: H, [G.C. 25262a], 1940, (105).
nygaardii Camburn in Camburn & Kingston: H, [G.C. 54240], 1983, (16).
pella Lohman & Andrews: I, [G.C. 63058], 1968, (90).
perglabra var. *floriniae* Camburn in Camburn & Kingston: H, [G.C. 54239], 1986, (16).
peudoamericana Camburn in Camburn & Kingston: H, [G.C. 54238], 1986, (16).
vitrea Lohman & Andrews: I, [G.C. 63058], 1968, (90).

Microsiphona

potamos Weber: P, [G.C. 51575], 1970, (179).

Minutocellus

pseudopolymorphus Hasle, von Stosch & Syvertsen: I, [G.C. 95358], 1983, (51).
scriptus Hasle, von Stosch & Syvertsen: I, [G.C. 95359], 1983, (51).

Navicula

achthera Hohn & Hellerman: H, [G.C. 44467], 1963, (60).
admenda Hohn & Hellerman: H, [G.C. 44453], 1963, (60).
adumbrata Hohn & Hellerman: H, [G.C. 44453], 1963, (60).
aglaos Hohn: H, [G.C. 25861a], 1966, (58).
agma Hohn & Hellerman: H, [G.C. 44450], 1963, (60).
agmastriata Hohn & Hellerman: I, [G.C. 44905], 1966, (61).
agmastriata Hohn & Hellerman: H, [G.C. 44905a], 1966, (61).
aikenensis Patrick: H, [G.C. 4737a], 1959, (113).
aikenensis Patrick: I, [G.C. 4737b], 1959, (113).
aktinoides Skuja: I*, [G.C. 35189a], 1937, (157).
aktinoides Skuja: I*, [G.C. 35189b], 1937, (157).
alaskana Patrick & Freese: H, [G.C. 8262a], 1961, (119).

Navicula (continued)

alaskana Patrick & Freese: I, [G.C. 8262b], 1961, (119).
alea Hohn & Hellerman: H, [G.C. 44466], 1963, (60).
algor Hohn & Hellerman: H, [G.C. 44450], 1963, (60).
allista Hohn & Hellerman: H, [G.C. 44890], 1966, (61).
americana var. *alastos* Hohn & Hellerman: H, [G.C. 44450], 1963, (60).
americana var. *moesta* Tempère & Peragallo: L, [T&P II 159], 1908, (167), **Design.**: Patrick in Patrick & Reimer, 1966, (120).
amnicola Hohn & Hellerman: H, [G.C. 44458], 1963, (60).
amphibola var. *arctica* Patrick & Freese: I, [G.C. 8262a], 1961, (119).
amphibola var. *arctica* Patrick & Freese: H, [G.C. 8262b], 1961, (119).
anatis Hohn & Hellerman: H, [G.C. 44467], 1963, (60).
ardis Hohn: H, [G.C. 25859a], 1966, (58).
arenula Hohn & Hellerman: H, [G.C. 44450], 1963, (60).
argutiola Hohn & Hellerman: H, [G.C. 44458], 1963, (60).
asymbasia Hohn & Hellerman: H, [G.C. 44469], 1963, (60).
atacamana Patrick: H, [G.C. 26098a], 1961, (114).
atacamana Patrick: I, [G.C. 26098b], 1961, (114).
atacamana Patrick: I, [G.C. 26098c], 1961, (114).
atalos Hohn: H, [G.C. 25862a], 1966, (58).
bacula Hohn & Hellerman: H, [G.C. 44452], 1963, (60).
barrowiana Patrick & Freese: I, [G.C. 8141a], 1961, (119).
barrowiana Patrick & Freese: H, [G.C. 8141b], 1961, (119).
barrowiana Patrick & Freese: I, [G.C. 8141c], 1961, (119).
barrowiana Patrick & Freese: I, [G.C. 8141d], 1961, (119).
barrowiana Patrick & Freese: I, [G.C. 8141e], 1961, (119).
barrowiana Patrick & Freese: I, [G.C. 8141f], 1961, (119).
bdesma Hohn: H, [G.C. 44489], 1961, (57).
bergeni Hohn: I, [G.C. 4148a], 1952, (56).
bergeni Hohn: I, [G.C. 4148b], 1952, (56).
biconica Patrick: H, [G.C. 44492], 1959, (113).
bievexa Hohn: H, [G.C. 44489], 1961, (57).
bifax Hohn & Hellerman: H, [G.C. 44913], 1966, (61).
binodulosa Sullivan & Reimer: H, [G.C. 53119], 1975, (163).
birhis Hohn: H, [G.C. 44484], 1961, (57).
bisulcata Lagerstedt var. *bisulcata*: I*, [G.C. 92512], 1873, (84).
bisulcata Lagerstedt var. *bisulcata*: I*, [G.C. 92539], 1873, (84).
bita Hohn: H, [G.C. 44474], 1961, (57).
bryophiloides Manguin in Bourrelly & Manguin var. *bryophiloides*: I*, [G.C. 91506], 1954, (10).
buccella Hohn & Hellerman: H, [G.C. 44453], 1963, (60).
canalis Patrick: H, [G.C. 25741], 1944, (109).
canoris Hohn & Hellerman: H, [G.C. 44469], 1963, (60).
capsa Hohn: H, [G.C. 44474], 1961, (57).
caractacus Hohn & Hellerman: H, [G.C. 44469], 1963, (60).
caroliniana Patrick: H, [G.C. 44496], 1959, (113).

Navicula (continued)

carvajaliana var. *attenuata* Patrick: H, [G.C. 26099a], 1961, (114).
carvajaliana var. *attenuata* Patrick: I, [G.C. 26099b], 1961, (114).
carvajaliana Patrick var. *carvajaliana*: H, [G.C. 26098a], 1961, (114).
carvajaliana Patrick var. *carvajaliana*: I, [G.C. 26098b], 1961, (114).
carvajaliana Patrick var. *carvajaliana*: I, [G.C. 26098c], 1961, (114).
caterva Hohn & Hellerman: H, [G.C. 44466], 1963, (60).
caupulus Hohn: H, [G.C. 25862a], 1966, (58).
cerneutia Hohn: H, [G.C. 44484], 1961, (57).
cincta var. *rostrata* Reimer: H, [G.C. 45669], 1961, (142).
cinna Hohn & Hellerman: H, [G.C. 44470], 1963, (60).
clevii Lagerstedt: I*, [G.C. 92511], 1873, (84).
cocconeiformis var. *parva* McCall: I, [G.C. 11061a], 1933, (96).
cocconeiformis var. *parva* McCall: I, [G.C. 11061b], 1933, (96).
concava Patrick: H, [G.C. 2188], 1945, (110).
conveniens var. *rostrata* Hohn: H, [G.C. 25862a], 1966, (58).
corrugata Manguin Bourrelly & Manguin: I*, [G.C. 91506], 1954, (10).
crateri Patrick: H, [G.C. 26618a], 1970, (117).
crateri Patrick: I, [G.C. 26618b], 1970, (117).
crateri Patrick: I, [G.C. 26618c], 1970, (117).
crateri Patrick: I, [G.C. 26618d], 1970, (117).
cremorne Hohn & Hellerman var. *cremorne*: H, [G.C. 44467], 1963, (60).
creuzburgensis var. *multistriata* Patrick: H, [G.C. 6679a], 1959, (113).
creuzburgensis var. *multistriata Patrick*: I, [G.C. 6679b], 1959, (113).
crucicula var. *alaskana* Patrick & Freese: H, [G.C. 8174a], 1961, (119).
crucicula var. *alaskana* Patrick & Freese: I, [G.C. 8174b], 1961, (119).
crucicula var. *barrowiana* Patrick & Freese: H, [G.C. 8203], 1961, (119).
cryptocephala var. *australis* Skuja: I*, [G.C. 35191a], 1937, (157).
cryptocephala var. *australis* Skuja: I*, [G.C. 35191b], 1937, (157).
cryptogaster Lowe: I, [G.C. 52650], 1972, (91).
cumvibia Hohn & Hellerman: H, [G.C. 44904], 1966, (61).
cuspidata var. *obtusa* Patrick in Patrick & Reimer: H, [Boy. A-VI-15], 1966, (120).
dailyi Reimer: H, [G.C. 45669], 1961, (142).
delastriata Hohn & Hellerman: H, [G.C. 44896], 1966, (61).
descripta var. *arctica* Patrick & Freese: H, [G.C. 8241a], 1961, (119).
descripta var. *arctica* Patrick & Freese: I, [G.C. 8241b], 1961, (119).
descripta var. *arctica* Patrick & Freese: I, [G.C. 8241c], 1961, (119).
dibola Hohn: H, [G.C. 44487], 1961, (57).
disculus Schumann: I*, [G.C. 11985], 1864, (154).
disputans Patrick: H, [G.C. 44496], 1959, (113).
distinctastriata Hohn & Hellerman: H, [G.C. 44468], 1963, (60).
divergens var. *bacillaris* M. Peragallo in Tempère & Peragallo: L, [T&P II 106], 1908, (167), **Design.:** Patrick in Patrick & Reimer, 1966, (120).

Navicula (continued)

drouetiana Patrick: H, [G.C. 25735], 1944, (109).
dulcis Patrick: H, [G.C. 8035], 1959, (113).
duomedia Patrick: H, [G.C. 44264a], 1959, (113).
duomedia Patrick: I, [G.C. 44264b], 1959, (113).
dystrophica Patrick: H, [G.C. 44254a], 1959, (113).
dystrophica Patrick: I, [G.C. 44254b], 1959, (113).
ebor Hohn & Hellerman: H, [G.C. 44470], 1963, (60).
elaphros Hohn & Hellerman: H, [G.C. 44453], 1963, (60).
elmorei Patrick in Patrick & Reimer: H, [CJElmore 704 N], 1966, (120).
elsoniana Patrick & Freese: H, [G.C. 8215a], 1961, (119).
elsoniana Patrick & Freese: I, [G.C. 8215b], 1961, (119).
entoleia var. *minor* Patrick & Freese: I, [G.C. 8153a], 1961, (119).
entoleia var. *minor* Patrick & Freese: I, [G.C. 8153b], 1961, (119).
entoleia var. *minor* Patrick & Freese: I, [G.C. 8153c], 1961, (119).
entoleia var. *minor* Patrick & Freese: H, [G.C. 8153d], 1961, (119).
eponka Hohn: H, [G.C. 44491], 1961, (57).
exigua var. *capitata* Patrick: H, [G.C. 2200], 1945, (110).
flavasinensis Moghadam: H, [G.C. 62270], 1969, (99).
fluminitica Camburn in Camburn, Lowe and Stoneburner: H, [G.C. 53748], 1978, (18).
freesei Patrick & Freese: H, [G.C. 8188a], 1961, (119).
freesei Patrick & Freese: I, [G.C. 8188b], 1961, (119).
friesneri Reimer: H, [G.C. 45669], 1961, (142).
gallica var. *montana* Bahls: I, [G.C. 63068], 1981, (6).
gallica var. *montana* Bahls: I, [G.C. 63069], 1981, (6).
gaufinii Moghadam: H, [G.C. 62228], 1969, (99).
germainii Wallace: H, [G.C. 42397a], 1960, (178).
germainii Wallace: I, [G.C. 42397b], 1960, (178).
goersii Bahls: H, [G.C. 63245], 1983, (8).
gravistriata Patrick: H, [G.C. 8031], 1959, (113).
habena Hohn & Hellerman: H, [G.C. 44452], 1963, (60).
hansenana Lee & Reimer: H, [G.C. 38082], 1984, (87).
hawaiiensis Johansen in Rushforth, Kaczmarska and Johansen: H, [G.C. 20313], 1984, (151).
hawaiiensis Johansen in Rushforth, Kaczmarska and Johansen: I, [G.C. 20314], 1984, (151).
hodgeana Patrick & Freese: H, [G.C. 8249a], 1961, (119).
hodgeana Patrick & Freese: I, [G.C. 8249b], 1961, (119).
hungarica var. *arctica* Patrick & Freese: I, [G.C. 8251a], 1961, (119).
hungarica var. *arctica* Patrick & Freese: I, [G.C. 8251b], 1961, (119).
hungarica var. *arctica* Patrick & Freese: H, [G.C. 8251c], 1961, (119).
hutchinsonii Patrick: H, [G.C. 13661], 1970, (116).
imbellis Hohn & Hellerman: H, [G.C. 44460], 1963, (60).
impertila Hohn & Hellerman: H, [G.C. 44894], 1966, (61).
incomitatus Hohn & Hellerman: H, [G.C. 44450], 1963, (60).

Navicula (continued)

indemnis Hohn & Hellerman: H, [G.C. 44452], 1963, (60).
indianensis Reimer: H, [G.C. 45669], 1961, (142).
infrenis Hohn & Hellerman: H, [G.C. 44470], 1963, (60).
karsia Hohn: H, [G.C. 44491], 1961, (57).
keeleyi Patrick: H, [G.C. 2197], 1945, (110).
kisber Hohn & Hellerman: H, [G.C. 44450], 1963, (60).
kleerekoperi Patrick: H, [G.C. 25734], 1944, (109).
lacuna Patrick & Freese: H, [G.C. 8159a], 1961, (119).
lacuna Patrick & Freese: I, [G.C. 8159b], 1961, (119).
lacuna Patrick & Freese: I, [G.C. 8159c], 1961, (119).
lacuna Patrick & Freese: I, [G.C. 8159d], 1961, (119).
lacuna Patrick & Freese: I, [G.C. 8159e], 1961, (119).
lacunicola Patrick & Freese: H, [G.C. 8225a], 1961, (119).
lacunicola Patrick & Freese: I, [G.C. 8225b], 1961, (119).
lacustris Gregory var. *lacustris*: I, [Febiger 3203], 1856, (45).
lagerstedtii var. *palustris* f. *minores* Fusey: I, [G.C. 12957], 1951, (42).
lalia Hohn & Hellerman: H, [G.C. 44468], 1963, (60).
latelongitudinalis Patrick: H, [G.C. 44258a], 1959, (113).
latelongitudinalis Patrick: I, [G.C. 44258b], 1959, (113).
lateropunctata Wallace: H, [G.C. 4072a], 1960, (178).
lateropunctata Wallace: I, [G.C. 4072b], 1960, (178).
lindae Sullivan & Reimer: H, [G.C. 53118], 1975, (163).
litos Hohn & Hellerman: H, [G.C. 44466], 1963, (60).
lomastriata Hohn: H, [G.C. 25858a], 1966, (58).
lubbockii Hohn & Hellerman: H, [G.C. 8043a], 1961, (59).
lubbockii Hohn & Hellerman: I, [G.C. 8043b], 1961, (59).
luisii Patrick: H, [G.C. 26099a], 1961, (114).
luisii Patrick: I, [G.C. 26099b], 1961, (114).
lumbricastriata Hohn & Hellerman: H, [G.C. 44902], 1966, (61).
maculata var. *orbiculata* Patrick in Patrick & Reimer: H, [Ward B-36-16 N], 1966, (120).
marginestriata var. *arctica* Patrick & Freese: H, [G.C. 8266a], 1961, (119).
marginestriata var. *arctica* Patrick & Freese: I, [G.C. 8266b], 1961, (119).
maria Hohn: H, [G.C. 25857a], 1966, (58).
mediacomplexa Hohn & Hellerman: H, [G.C. 44450], 1963, (60).
mediahelos Hohn & Hellerman: H, [G.C. 44460], 1963, (60).
mediocris var. *intermedia* Reimer: H, [G.C. 44260a], 1966, (143).
mediocris var. *intermedia* Reimer: I, [G.C. 44260b], 1966, (143).
mica Hohn & Hellerman: H, [G.C. 44453], 1963, (60).
migma Hohn & Hellerman: H, [G.C. 44460], 1963, (60).
minthe Hohn & Hellerman: H, [G.C. 44469], 1963, (60).

Navicula (continued)

minuscula var. *minuscula* f. *linearis* Reimer: H, [G.C. 61083], 1970, (144).
mobiliensis var. *minor* Patrick: H, [G.C. 44497], 1959, (113).
mobiliensis Boyer var. *mobiliensis*: I, [G.C. 2955], 1922, (14).
monela Hohn: H, [G.C. 25858a], 1966, (58).
montanensis Moghadam: I, [G.C. 62310a], 1969, (99).
montanensis Moghadam: I, [G.C. 62310b], 1969, (99).
montanensis Moghadam: I, [G.C. 62310c], 1969, (99).
montanensis Moghadam: H, [G.C. 62310d], 1969, (99).
mournei Patrick: I, [Boy. 677], 1959, (113).
multigramma Hohn & Hellerman: H, [G.C. 44469], 1963, (60).
muscerda Hohn: H, [G.C. 44489], 1961, (57).
mutica var. *stigma* Patrick: H, [G.C. 3568a], 1959, (113).
mutica var. *stigma* Patrick: I, [G.C. 3568b], 1959, (113).
mutica var. *subhexagona* Playfair: I*, [G.C. 40025a], 1915, (122).
narinosa Hohn: H, [G.C. 44489], 1961, (58).
nemoris Hohn & Hellerman: H, [G.C. 44469], 1963, (60).
netroformis Andrews: I, [G.C. 63060], 1971, (5).
nimbus Hohn & Hellerman: H, [G.C. 44467], 1963, (60).
niobrara Andrews: I, [G.C. 63059], 1970, (4).
notha Wallace: I, [G.C. 4613a], 1960, (178).
notha Wallace: H, [G.C. 4613b], 1960, (178).
nugalis Hohn & Hellerman: H, [G.C. 44458], 1963, (60).
nunivakiana Patrick & Freese: H, [G.C. 8232a], 1961, (119).
nunivakiana Patrick & Freese: I, [G.C. 8232b], 1961, (119).
nuwukiana Patrick & Freese: H, [G.C. 8144], 1961, (119).
obdurata Hohn & Hellerman: H, [G.C. 4695a], 1963, (60).
obdurata Hohn & Hellerman: I, [G.C. 4695b], 1963, (60).
ocallii Hohn: H, [G.C. 44484], 1961, (57).
odiosa Wallace: H, [G.C. 6853a], 1960, (178).
odiosa Wallace: I, [G.C. 6853b], 1960, (178).
orangiana Patrick: H, [G.C. 6535a], 1959, (113).
orangiana Patrick: I, [G.C. 6535b], 1959, (113).
orbiculata Patrick: H, [G.C. 8030], 1959, (113).
orellana Hohn: H, [G.C. 25861a], 1966, (58).
paca Hohn & Hellerman: H, [G.C. 44453], 1963, (60).
paludosa var. *rhomboidea* Reimer: H, [G.C. 61083], 1970, (144).
panda Lohman & Andrews: I, [G.C. 63058], 1968, (90).
parablis Hohn & Hellerman: H, [G.C. 44466], 1963, (60).
parodia Hohn: H, [G.C. 44489], 1961, (57).
paucivisitata Patrick: H, [G.C. 44274a], 1959, (113).
paucivisitata Patrick: I, [G.C. 44274b], 1959, (113).
pelta Hohn: H, [G.C. 25862a], 1966, (58).
peregrina var. *producta* McCall: I*, [G.C. 11058], 1933, (96).

Navicula (continued)

peticolasii M. Peragallo in Tempère & Peragallo var. *peticolasii*: L, [T&P II 365], 1910, (168), {*Navicula (peregrina* var.?) *peticolasii* M. Peragallo}, 1910, (168)}, **Design.:** Patrick in Patrick & Reimer, 1966, (120).

phantasma Hohn: H, [G.C. 25859a], 1966, (58).

pletura Hohn: H, [G.C. 44474], 1961, (57).

poconoensis Patrick: H, [G.C. 2188], 1945, (110).

portanova Riznyk: H, [G.C. 62634], 1973, (149).

potzgeri Reimer var. *potzgeri*: H, [G.C. 45669], 1961, (142).

potzgeri var. *quadripunctata* Reimer: H, [G.C. 45669], 1961, (142).

pragma Hohn & Hellerman: H, [G.C. 44466], 1963, (60).

pseudofrickia Patrick: H, [J.Grant 16Nov1928 N], 1959, (112).

pseudominuscula Fusey: I*, [G.C. 12951], 1950, (42).

pseudosepta Patrick: H, [G.C. 26100a], 1961, (114).

radiosa var. *parva* Wallace: I, [G.C. 4373a], 1960, (178).

radiosa var. *parva* Wallace: H, [G.C. 4373b], 1960, (178).

recava Hohn & Hellerman: H, [G.C. 44469], 1963, (60).

reimeri Patrick & Freese: H, [G.C. 8289a], 1963, (119).

reimeri Patrick & Freese: I, [G.C. 8289b], 1961, (119).

reimerites Van Landingham: H, [G.C. 8518], 1964, (172).

reissii Lee, Reimer & McEnery: H, [G.C. 38062], 1980, (86).

rhodana Hohn & Hellerman: H, [G.C. 44451], 1963, (60).

rhynchocephala var. *germainii* (Wallace) Patrick in Patrick & Reimer: L, [G.C. 42397a], 1966, (120), {*Navicula germainii* Wallace, 1960, (178)}, **Tfr.:** & **Design.:** Patrick in Patrick & Reimer, 1966, (120).

rhynchocephala var. *germainii* (Wallace) Patrick in Patrick & Reimer: I, [G.C. 42397b], 1966, (120), {as: *Navicula germainii* Wallace, 1960, (178)}, **Tfr.:** & **Design.:** Patrick in Patrick & Reimer, 1966, (120).

rivalis Hohn & Hellerman: H, [G.C. 44458], 1963, (60).

rivulensis Patrick & Freese: H, [G.C. 8179a], 1961, (119).

rivulensis Patrick & Freese: I, [G.C. 8179b], 1961, (119).

robertsii Patrick & Freese: I, [G.C. 8189a], 1961, (119).

robertsii Patrick & Freese: I, [G.C. 8189b], 1961, (119).

robertsii Patrick & Freese: H, [G.C. 8189c], 1961, (119).

rotunda Andrews: I, [G.C. 53732], 1966, (3).

rugula Hohn & Hellerman: H, [G.C. 44472], 1963, (60).

sabiniana Patrick: H, [G.C. 8030], 1959, (113).

sagitta Hohn & Hellerman: H, [G.C. 44470], 1963, (60).

salaria Patrick & Freese: H, [G.C. 8131a], 1961, (119).

salaria Patrick & Freese: I, [G.C. 8131b], 1961, (119).

salinicola var. *boliviana* Patrick: H, [G.C. 26098a], 1961, (114).

salinicola var. *boliviana* Patrick: I, [G.C. 26098b], 1961, (114).

salinicola var. *boliviana* Patrick: I, [G.C. 26098c], 1961, (114).

Navicula (continued)

salsa Patrick & Freese: H, [G.C. 8182], 1961, (119).
scala Hohn & Hellerman: H, [G.C. 44891], 1966, (61).
scala Hohn & Hellerman: I, [G.C. 44891a], 1966, (61).
secreta var. *apiculata* Patrick: H, [G.C. 6604a], 1959, (113).
secreta var. *apiculata* Patrick: I, [G.C. 6604b], 1959, (113).
secura Patrick: H, [G.C. 44254a], 1959, (113).
secura Patrick: I, [G.C. 44254b], 1959, (113).
seminulum var. *hustedtii* Patrick: H, [G.C. 44254a], 1959, (113).
seminulum var. *hustedtii* Patrick: I, [G.C. 44254b], 1959, (113).
serpentina McCall: I, [G.C. 11055], 1933, (96).
setschwanensis Skuja: I, [G.C. 35190a], 1937, (157).
setschwanensis Skuja: I, [G.C. 35190b], 1937, (157).
setzeri Patrick & Freese: H, [G.C. 8288], 1961, (119).
silenda Hohn: H, [G.C. 25861a], 1966, (58).
simula Patrick: H, [G.C. 44259a], 1959, (113).
simula Patrick: I, [G.C. 44259b], 1959, (113).
sinuiraphe Patrick & Freese: I, [G.C. 8289a], 1961, (119).
sinuiraphe Patrick & Freese: H, [G.C. 8289b], 1961, (119).
skalenastriata Hohn: H, [G.C. 44474], 1961, (57).
socialis Palmer: I, [G.C. 45959], 1910, (104).
sorella Hohn & Hellerman: H, [G.C. 44453], 1963, (60).
spartinetensis Sullivan & Reimer: H, [G.C. 53120], 1975, (163).
stigmatifera John: H, [G.C. 40073], 1981, (70).
subfasciata Patrick: H, [G.C. 44259a], 1959, (113).
subfasciata Patrick: I, [G.C. 44259b], 1959, (113).
swaniana Moghadam: H, [G.C. 62306a], 1969, (99).
swaniana Moghadam: I, [G.C. 62306b], 1969, (99).
symmetrica Patrick var. *symmetrica*: H, [G.C. 25740], 1944, (109).
tagiana Patrick: H, [G.C. 26618a], 1970, (117).
tagiana Patrick: I, [G.C. 26618b], 1970, (117).
tagiana Patrick var. *tagiana*: I, [G.C. 26618c], 1970, (117).
tagiana Patrick: I, [G.C. 26618d], 1970, (117).
taraxa Hohn & Hellerman: H, [G.C. 44903], 1966, (61).
teleta Hohn: H, [G.C. 25862a], 1966, (58).
texana Patrick: H, [G.C. 6587a], 1959, (113).
thurstonensis Kaczmarska in Rushforth, Kaczmarska and Johansen: H, [G.C. 20315], 1984, (151).
thurstonensis Kaczmarska in Rushforth, Kaczmarska and Johansen: I, [G.C. 20316], 1984, (151).
thurstonensis Kaczmarska in Rushforth, Kaczmarska and Johansen: P, [G.C. 20317], 1984, (151).
tracery Hohn & Hellerman: H, [G.C. 44450], 1963, (60).
tripunctata var. *arctica* Patrick & Freese: I, [G.C. 8223a], 1961, (119).

Navicula (continued)

tripunctata var. *arctica* Patrick & Freese: H, [G.C. 8223b], 1961, (119).
tripunctata (O.F. Müller) Bory in Lamouroux, Bory and Deslongchamps var. *tripunctata*: N, [VanHeurck 81], 1824, (85), {*Vibrio tripunctatus* O.F. Müller, 1786, (101)}, **Tfr.**: Bory in Lamouroux, Bory and Deslongchamps, 1824, (85), **Design.**: Patrick, 1959, (113).
umbilicatissima Reichardt: I, [G.C. 15146], 1983, (139).
umbra Hohn & Hellerman: H, [G.C. 44469], 1963, (60).
vampyra Hohn: H, [G.C. 25858a], 1966, (58).
variostriata Krasske var. *variostriata*: I*, [G.C. 10637a], 1929, (78).
variostriata Krasske var. *variostriata*: I*, [G.C. 10637b], 1929, (78).
variostriata Krasske var. *variostriata*: I*, [G.C. 10637c], 1929, (78).
variostriata Krasske var. *variostriata*: I*, [G.C. 10637d], 1929, (78).
venerablis Hohn & Hellerman: H, [G.C. 44458], 1963, (60).
vitabunda var. *montanensis* Moghadam: I, [G.C. 62304a], 1969, (99).
vitabunda var. *montanensis* Moghadam: H, [G.C. 62304b], 1969, (99).
walkeri Patrick & Freese: H, [G.C. 8188a], 1961, (119).
wallacei Reimer: H, [G.C. 4628a], 1966, (143).
wallacei Reimer: I, [G.C. 4628b], 1966, (143).
wardii Patrick: H, [Ward D-4-21 N], 1959, (112).
wigginsiana Patrick & Freese: I, [G.C. 8208a], 1961, (119).
wigginsiana Patrick & Freese: H, [G.C. 8208b], 1961, (119).
yorkensis Camburn in Camburn, Lowe and Stoneburner: H, [G.C. 53747], 1978, (18).

Neidium

affine var. *humerus* Reimer in Patrick & Reimer: H, [G.C. 44285a], 1966, (120).
affine var. *humerus* Reimer in Patrick & Reimer: I, [G.C. 44285b], 1966, (120).
amphigomphus var. *intermedium* McCall: I, [G.C. 11063a], 1933, (96).
amphigomphus var. *intermedium* McCall: I, [G.C. 11063b], 1933, (96).
apiculatum Reimer var. *apiculatum*: I, [G.C. 44266a], 1959, (140).
apiculatum Reimer var. *apiculatum*: I, [G.C. 44266b], 1959, (140).
apiculatum Reimer var. *apiculatum*: H, [G.C. 44266c], 1959, (140).
apiculatum var. *constrictum* Reimer: I, [G.C. 44266a], 1959, (140).
apiculatum var. *constrictum* Reimer: H, [G.C. 44266b], 1959, (140).
apiculatum var. *constrictum* Reimer: I, [G.C. 44266c], 1959, (140).
aubertii Manguin in Bourrelly & Manguin: I*, [G.C. 91506], 1954, (10).
bisulcatum var. *baicalensis* (Skvortzov & Meyer) Reimer: N, [G.C. 44152], 1959, (140), {*Neidium bisulcatum* f. *baicalensis* Skvortzov & Meyer, 1928, (159), **Tfr.**: & **Design.**: Reimer, 1959, (140).

Neidium (continued)

bisulcatum (Lagerstedt) Cleve var. *bisulcatum*: I, [G.C. 92512], 1880, (26), {*Navicula bisulcata* Lagerstedt var. *bisulcata*, *1873, (84)*}, **Tfr.:** *Cleve, 1880, (26).*

bisulcatum (Lagerstedt) Cleve var. *bisulcatum*: I, [G.C. 92539], 1880, (26), {*Navicula bisulcata* Lagerstedt var. *bisulcata*, *1873, (84)*}, **Tfr.:** *Cleve, 1880, (26).*

bisulcatum var. *nipponicum* Skvortzov: N, [G.C. 3460a], 1937, (158), **Design.:** Reimer, 1959, (140).

boyeri Reimer: H, [Boy. 778], 1959, (140).

calvum Østrup: I, [G.C. 12566], 1910, (103).

capitatum McCall: I, [G.C. 11063a], 1933, (96).

capitatum McCall: I, [G.C. 11063b], 1933, (96).

fasciatum var. *denudatum* Østrup: I, [G.C. 11648], 1910, (103).

fasciatum var. *denudatum* Østrup: I, [G.C. 12565], 1910, (103).

fasciatum Østrup var. *fasciatum*: I, [G.C. 12570], 1910, (103).

floridanum Reimer: I, [G.C. 44155a], 1959, (140).

floridanum Reimer: H, [G.C. 44155b], 1959, (140).

hercynicum A. Mayer var. *hercynicum*: N, [A. Mayer 905 Coll. Holzheim R], 1917, (95), **Design.:** Reimer, 1959, (140).

hercynicum var. *hercynicum* f. *subrostratum* Wallace ex Reimer: H, [G.C. 3984a], 1959, (140).

incurvum (Gregory) Østrup var. *incurvum*: I, [Febiger 3471], 1910, (103), {*Navicula incurva* Gregory var. *incurva*, 1856, (45)}, **Tfr.:** Østrup, 1910, (103).

iridis var. *bryophilum* McCall: I*, [G.C. 11055], 1933, (96).

iridis var. *bryophilum* McCall: I*, [G.C. 11056a], 1933, (96).

iridis var. *bryophilum* McCall: I*, [G.C. 11056b], 1933, (96).

iridis var. *robusta* McCall: I, [G.C. 11063a], 1933, (96).

iridis var. *robusta* McCall: I, [G.C. 11063b], 1933, (96).

knuthii var. *heilprinensis* Foged: I, [G.C. 90003], 1955, (37).

knuthii Foged var. *knuthii*: I, [G.C. 90003], 1955, (37).

knuthii var. *marraitensis* Foged: I, [G.C. 92683], 1964, (39).

kozlowi var. *baicalensis* f. *robusta* Stoermer: H, [G.C. 8301], 1963, (162).

kozlowi var. *rostrata* f. *subrostrata* Fusey: I, [G.C. 12957], 1951, (42).

kozlowi var. *undulata* Stoermer: H, [G.C. 8299a], 1963, (162).

kozlowi var. *undulata* Stoermer: I, [G.C. 8299b], 1963, (162).

ladogense var. *densestriatum* f. *peribryum* Lowe & Kociolek: H, [G.C. 53919], 1984, (92).

ladogense var. *densistriatum* (Østrup) Foged: I*, [G.C. 12568], 1952, (36), {*Caloneis ladogensis* var. *densistriata* Østrup, 1910, (103)}, **Tfr.:** Foged, 1952, (36).

maculatum Maillard: I, [G.C. 12954a], 1962, (93).

maculatum Maillard: I, [G.C. 12954b], 1962, (93).

Neidium (continued)

maculatum Maillard: I, [G.C. 12955], 1962, (93).
munckii Foged: I, [G.C. 90003], 1955, (37).
opacelineatum Riznyk: H, [G.C. 62634], 1973, (149).
reimeri John: H, [G.C. 40071], 1981, (68).
roenningii Foged: I, [G.C. 92681], 1964, (39).
rosenkrantzii Foged: I, [G.C. 90037], 1958, (38).
rudimentarum Reimer: H, [Boy. W-VI-23], 1959, (140).
sacoense Reimer: H, [Shulze A 367], 1959, (140).
spitzbergense Foged: I, [G.C. 92682], 1964, (39).
temperei Reimer: H, [T&P II 211], 1959, (140).
tenue Østrup: I, [G.C. 11647], 1910, (103).
tenue Østrup: I, [G.C. 12567], 1910, (103).

Neostreptotheca

subindica von Stosch: I, [G.C. 17124], 1980, (175).

Nitzschia

abridia Camburn in Camburn, Lowe and Stoneburner: H, [G.C. 53750], 1978, (18).
accedens var. *chilensis* Patrick: H, [G.C. 26099a], 1961, (114).
accedens var. *chilensis* Patrick: I, [G.C. 26099b], 1961, (114).
acicularis var. *adelos* Hohn & Hellerman: H, [G.C. 44469], 1963, (60).
alaskana Patrick & Freese: H, [G.C. 8207a], 1961, (119).
alaskana Patrick & Freese: I, [G.C. 8207b], 1961, (119).
amphibioides var. *guatemalensis* Patrick: H, [G.C. 30656], 1966, (115).
asymbasia Hohn: H, [G.C. 44474], 1961, (57).
barca Hohn & Hellerman: H, [G.C. 44902], 1966, (61).
barrowiana Patrick & Freese: H, [G.C. 8121a], 1961, (119).
barrowiana Patrick & Freese: I, [G.C. 8121b], 1961, (119).
beagleana Patrick: H, [G.C. 26620a], 1970, (117).
beagleana Patrick: I, [G.C. 26620b], 1970, (117).
beagleana Patrick: I, [G.C. 26620c], 1970, (117).
biacrula Hohn & Hellerman: H, [G.C. 44466], 1963, (60).
bicrena Hohn & Hellerman: H, [G.C. 44460], 1963, (60).
bita Hohn & Hellerman: H, [G.C. 3628a], 1963, (60).
bita Hohn & Hellerman: I, [G.C. 3628b], 1963, (60).
bulnheimiana var. *capitata* Reimer: H, [G.C. 44264a], 1966, (143).
bulnheimiana var. *capitata* Reimer: I, [G.C. 44264b], 1966, (143).
clausii Hantzsch in Rabenhorst var. *clausii*: I, [G.C. 10446], 1860, (129).
clausii Hantzsch in Rabenhorst var. *clausii*: I, [G.C. 10477], 1860, (129).
clausii Hantzsch in Rabenhorst var. *clausii*: I, [G.C. 11257], 1860, (129).
communis Rabenhorst var. *communis*: I, [G.C. 10426], 1860, (129).

Nitzschia (continued)

communis Rabenhorst var. *communis*: I, [G.C. 10427], 1860, (129).
communis Rabenhorst var. *communis*: I, [G.C. 11264], 1860, (129).
confinis var. *maxima* Patrick: H, [G.C. 26620a], 1970, (117).
confinis var. *maxima* Patrick: I, [G.C. 26620b], 1970, (117).
confinis var. *maxima* Patrick: I, [G.C. 26620c], 1970, (117).
congolensis var. *mooreae* Reimer: H, [ILL L-2-90 I], 1982, (145).
copiastriata Hohn & Hellerman: H, [G.C. 44907], 1966, (61).
cryptostriata Hohn & Hellerman: H, [G.C. 44896], 1966, (61).
cylindroformis Hasle in Hasle & Booth: I, [G.C. 20311], 1984, (50).
firthii Fuge: I, [G.C. 326], 1937, (40).
fluvialis Patrick & Freese: H, [G.C. 8160], 1961, (119).
fremontensis Lohman & Andrews: I, [G.C. 63058], 1968, (90).
frustulum var. *kerguelenensis* Manguin in Bourrelly & Manguin: I*, [G.C. 91506], 1954, (10).
frustulum var. *symbiotica* Lee & Reimer: H, [G.C. 38083], 1984, (87).
grana Hohn & Hellerman: H, [G.C. 44906], 1966, (61).
hantzschiana Rabenhorst var. *hantzschiana*: I, [G.C. 11256], 1860, (129).
hulensis Sherman & Patrick: H, [G.C. 38064], 1981, (156).
ignorata var. *ignorata* f. *longissima* Manguin in Bourrelly & Manguin: I*, [G.C. 91506], 1954, (10).
incomptus Hohn & Hellerman var. *incomptus*: H, [G.C. 44469], 1963, (60).
kuetzingiana Hilse in Rabenhorst var. *kuetzingiana*: I, [G.C. 11377], 1862, (132).
lacuna Patrick & Freese: H, [G.C. 8158], 1961, (119).
lacunicola Patrick & Freese: H, [G.C. 8121a], 1961, (119).
limulus Hohn & Hellerman: H, [G.C. 44450], 1963, (60).
magnacarina Hohn & Hellerman: H, [G.C. 44906], 1966, (61).
media Hantzsch in Rabenhorst: I, [G.C. 13128], 1860, (129).
mediastalsis Hohn & Hellerman: H, [G.C. 44450], 1963, (60).
minuta Bleisch in Rabenhorst var. *minuta*: I, [G.C. 10428], 1860, (129).
minuta Bleisch in Rabenhorst var. *minuta*: I, [G.C. 10429], 1860, (129).
minuta Bleisch in Rabenhorst var. *minuta*: I, [G.C. 11265], 1860, (129).
montanestris Camburn in Camburn Lowe, and Stoneburner: H, [G.C. 53749], 1978, (18).
nuwukiana Patrick & Freese: I, [G.C. 8179a], 1961, (119).
nuwukiana Patrick & Freese: H, [G.C. 8179b], 1961, (119).
obtusa var. *multistriata* Hohn: H, [G.C. 25861a], 1966, (58).
paradoxa var. *perpusilla* Playfair: I*, [G.C. 40023a], 1915, (122).
paradoxa var. *perpusilla* Playfair: I*, [G.C. 40027a], 1915, (122).
perspicillata Camburn in Camburn, Lowe and Stoneburner: H, [G.C. 53751], 1978, (18).
pertica Hohn & Hellerman: H, [G.C. 44467], 1963, (60).
pisca Patrick & Freese: H, [G.C. 8174a], 1961, (119).
pisca Patrick & Freese: I, [G.C. 8174b], 1961, (119).

Nitzschia (continued)

rangoonensis Grunow in Rabenhorst: I, [G.C. 35158], 1873, (136).
recta Hantzsch in Rabenhorst var. *recta*: I, [G.C. 11085], 1862, (133).
recta Hantzsch in Rabenhorst var. *recta*: I, [G.C. 11381], 1862, (133).
semidesum Hohn & Hellerman: H, [G.C. 44468], 1963, (60).
sentiformis Hohn & Hellerman: H, [G.C. 44469], 1963, (60).
sigma var. *undulata* Hohn & Hellerman: H, [G.C. 44898], 1966, (61).
silicula var. *commutata* Reimer: H, [G.C. 44258a], 1966, (143).
silicula var. *commutata* Reimer: I, [G.C. 44258b], 1966, (143).
silicula var. *commutata* Reimer: I, [G.C. 44258c], 1966, (143).
tryblionella var. *recta* McCall: I, [G.C. 11054a], 1933, (96).
tryblionella var. *recta* McCall: I, [G.C. 11054b], 1933, (96).
tryblionella var. *recta* McCall: I, [G.C. 11054c], 1933, (96).
tumulana Patrick & Freese: H, [G.C. 8139a], 1961, (119).
vermicularis var. *sialis* Playfair: I*, [G.C. 40026a], 1915, (122).

Odontella

retiformis var. *trigona* von Stosch: I, [G.C. 40099], 1985, (176).

Opephora

ansata Hohn & Hellerman: H, [G.C. 44468], 1963, (60).
linearis Sherman & Patrick: H, [G.C. 38065], 1981, (156).

Papiliocellulus

elegans Hasle, von Stosch & Syvertsen: I, [G.C. 95360], 1983, (51).

Peronia

intermedium (H.L. Smith) Patrick in Patrick & Reimer: L, [H.L.Sm.EX 238], 1966, (120), {*Meridion intermedium* H.L. Smith, 1878, (160)}, **Tfr.**: & **Design.**: Patrick in Patrick & Reimer, 1966, (120).

Pinnularia

absita Hohn & Hellerman: H, [G.C. 44453], 1963, (60).
aequilateralis Patrick & Freese: H, [G.C. 8141a], 1961, (119).
aequilateralis Patrick & Freese: I, [G.C. 8141b], 1961, (119).
aequilateralis Patrick & Freese: I, [G.C. 8141c], 1961, (119).
aequilateralis Patrick & Freese: I, [G.C. 8141d], 1961, (119).
aequilateralis Patrick & Freese: I, [G.C. 8141e], 1961, (119).
aequilateralis Patrick & Freese: I, [G.C. 8141f], 1961, (119).
alaskana Patrick & Freese: I, [G.C. 8215a], 1961, (119).
alaskana Patrick & Freese: H, [G.C. 8215b], 1961, (119).
alpina Wm. Smith var. *alpina*: I*, [Wm.Smith 115], 1853, (161).
amblys Hohn & Hellerman: H, [G.C. 44469], 1963, (60).
aquilonaris Hohn & Hellerman: H, [G.C. 44450], 1963, (60).
backebergii Manguin in Bourrelly & Manguin: I, [G.C. 91506], 1954, (10).

Pinnularia (continued)

barca Lohman & Andrews: I, [G.C. 63058], 1968, (90).
barrowiana Patrick & Freese: H, [G.C. 8283b], 1961, (119).
birnirkiana Patrick & Freese: H, [G.C. 8215a], 1961, (119).
birnirkiana Patrick & Freese: I, [G.C. 8215b], 1961, (119).
bogotensis (Grunow) Cleve var. *bogotensis*: L, [H.L.Sm.EX 681], 1895, (25), {*Navicula bogotensis* Grunow var. *bogotensis*, 1876, (152)}, **Tfr.**: Cleve, 1895, (25), **Design.**: Patrick in Patrick & Reimer, 1966, (120).
borealis var. *cuneorostrata* Manguin in Bourrelly & Manguin: I, [G.C. 91506], 1954, (10).
boyeri Patrick in Patrick & Reimer: H, [Boy. V-V-5], 1966, (120).
burkii Patrick var. *burkii*: H, [G.C. 2189], 1945, (110).
castor Hohn & Hellerman: H, [G.C. 44450], 1963, (60).
caudata (Boyer) Patrick in Patrick & Reimer: L, [Boy. V-V-2], 1966, (120). {*Pinnularia viridis* var. *caudata* Boyer, 1916, (12)}, **Tfr.** & **Design.**: Patrick in Patrick & Reimer, 1966, (120).
celtica Fusey: I, [G.C. 12957], 1951, (42).
circumducta Manguin in Bourrelly & Manguin: I, [G.C. 91506], 1954, (10).
clevei Patrick: H, [G.C. 2225], 1945, (110).
cumvibia Hohn & Hellerman: H, [G.C. 44458], 1963, (60).
cuneola Reichardt: I, [G.C. 15145], 1981, (138).
differentialis Patrick & Freese: H, [G.C. 8263a], 1961, (119).
divergens var. *bacillaris* (M. Peragallo) Mills: L, [T&P II 106], 1934, (98), {*Navicula divergens* var. *bacillaris* M. Peragallo, 1908, (167)}, **Tfr.**: Mills, 1934, (98), **Design.**: Patrick in Patrick & Reimer, 1966, (120).
doloma Hohn & Hellerman: H, [G.C. 44450], 1963, (60).
elliptica Lohman & Andrews: I, [G.C. 63058], 1968, (90).
fluminea Patrick & Freese: I, [G.C. 8197a], 1961, (119).
fluminea Patrick & Freese: I, [G.C. 8197b], 1961, (119).
fluminea Patrick & Freese: I, [G.C. 8197c], 1961, (119).
fluminea Patrick & Freese: H, [G.C. 8197d], 1961, (119).
fusana Andrews: I, [G.C. 63060], 1971, (5).
gibba var. *gibba* f. *curta* Bleisch in Rabenhorst: I, [G.C. 10430], 1860, (129).
gibba var. *gibba* f. *curta* Bleisch in Rabenhorst: I, [G.C. 10431], 1860, (129).
gibba var. *rostrata* Patrick: H, [G.C. 2213], 1945, (110).
gnoma Lohman & Andrews: I, [G.C. 63058], 1968, (90).
hagelsteinia Boyer: I, [G.C. 60858], 1920, (13).
institа Hohn & Hellerman: H, [G.C. 44458], 1963, (60).
irregularis Lohman & Andrews: I, [G.C. 63058], 1968, (90).
kaolakiana Patrick & Freese: I, [G.C. 8281a], 1961, (119).
kaolakiana Patrick & Freese: H, [G.C. 8281b], 1961, (119).

Pinnularia (continued)

kolbei Manguin in Bourrelly & Manguin: I*, [G.C. 91506], 1954, (10).
lacunicola Patrick & Freese: I, [G.C. 8159a], 1961, (119).
lacunicola Patrick & Freese: I, [G.C. 8159b], 1961, (119).
lacunicola Patrick & Freese: H, [G.C. 8159c], 1961, (119).
lacunicola Patrick & Freese: I, [G.C. 8159d], 1961, (119).
lacunicola Patrick & Freese: I, [G.C. 8159e], 1961, (119).
leptosoma var. *arctica* Patrick & Freese: I, [G.C. 8141a], 1961, (119).
leptosoma var. *arctica* Patrick & Freese: I, [G.C. 8141b], 1961, (119).
leptosoma var. *arctica* Patrick & Freese: H, [G.C. 8141c], 1961, (119).
leptosoma var. *arctica* Patrick & Freese: I, [G.C. 8141d], 1961, (119).
leptosoma var. *arctica* Patrick & Freese: I, [G.C. 8141e], 1961, (119).
leptosoma var. *arctica* Patrick & Freese: I, [G.C. 8141f], 1961, (119).
macrostauron Patrick & Freese: H, [G.C. 8176a], 1961, (119).
macrostauron Patrick & Freese: I, [G.C. 8176b], 1961, (119).
magnaconvexa John: I, [G.C. 40026a], 1981, (68).
magnaconvexa John: H, [G.C. 40026b], 1981, (68).
maior var. *pulchella* Boyer: L, [Boy. 426], 1916, (12), {*Pinnularia major* var. *pulchella* Boyer}, 1916, (12), **Design.:** Patrick in Patrick & Reimer, 1966, (120).
major var. *dubia* McCall: I*, [G.C. 11061a], 1933, (96).
major var. *dubia* McCall: I*, [G.C. 11061b], 1933, (96).
major var. *heribaudii* McCall: I, [G.C. 11056], 1933, (96).
nuwukiana Patrick & Freese: H, [G.C. 8179a], 1961, (119).
nuwukiana Patrick & Freese: I, [G.C. 8179b], 1961, (119).
obesa Lohman & Andrews: I, [G.C. 63058], 1968, (90).
orellana Hohn: H, [G.C. 25862a], 1966, (58).
quadratarea var. *dulcicola* Manguin in Bourrelly & Manguin: I*, [G.C. 91506], 1954, (10).
rigens var. *arctica* Patrick & Freese: I, [G.C. 8283a], 1961, (119).
rigens var. *arctica* Patrick & Freese: H, [G.C. 8283b], 1961, (119).
runa Lohman & Andrews: I, [G.C. 63058], 1968, (90).
rupestris Hantzsch in Rabenhorst: L, [G.C. 11084], 1861, (131), **Design.:** Patrick in Patrick & Reimer, 1966, (120).
scapha Lohman & Andrews: I, [G.C. 63058], 1968, (90).
semicruciata var. *arctica* Patrick & Freese: H, [G.C. 8192], 1961, (119).
serpentina Lohman & Andrews: I, [G.C. 63058], 1968, (90).
spatula Lohman & Andrews: I, [G.C. 63058], 1968, (90).
steereana Patrick & Freese: H, [G.C. 8166a], 1961, (119).
steereana Patrick & Freese: I, [G.C. 8166b], 1961, (119).
stenostriata Patrick & Freese: H, [G.C. 8143], 1961, (119).
subrostrata Lohman & Andrews: I, [G.C. 63058], 1968, (90).
subsolaris var. *subsolaris* f. *kerguelenensis* Manguin in Bourrelly & Manguin: I*, [G.C. 91506], 1954, (10).

Pinnularia (continued)

sudetica Hilse var. *sudetica*: L, [G.C. 11806], 1860, (55), **Design.**: Patrick in Patrick & Reimer, 1966, (120).
tenuiraphe Patrick & Freese: H, [G.C. 8170], 1961, (119).
tumida Lohman & Andrews: I, [G.C. 63058], 1968, (90).
westii McCall: I, [G.C. 11062a], 1933, (96).
westii McCall: I, [G.C. 11062b], 1933, (96).
yaquinensis Riznyk: H, [G.C. 62634], 1973, (149).

Plagiotropis

arizonica Czarnecki & Blinn: H, [G.C. 61229], 1978, (30).
arizonica Czarnecki & Blinn: I, [G.C. 61230], 1978, (30).
arizonica Czarnecki & Blinn: I, [G.C. 61231], 1978, (30).
arizonica Czarnecki & Blinn: I, [G.C. 61232], 1978, (30).

Pleurosigma

angulatum var. *robusta* McCall: I*, [G.C. 11054a], 1933, (96).
angulatum var. *robusta* McCall: I*, [G.C. 11054b], 1933, (96).
angulatum var. *robusta* McCall: I*, [G.C. 11054c], 1933, (96).
delicatulum var. *gracile* McCall: I*, [G.C. 11058], 1933, (96).
obtusatum Sullivant in Sullivant & Wormley: I, [Boy. W-VI-20], 1859, (164).
obtusatum Sullivant in Sullivant & Wormley: I, [Boy. W-VI-21], 1859, (164).
obtusatum Sullivant in Sullivant & Wormley: I, [Febiger 3657], 1859, (164).
obtusatum Sullivant in Sullivant & Wormley: I, [Febiger 3660], 1859, (164).
obtusatum Sullivant in Sullivant & Wormley: I, [Febiger 4474], 1859, (164).
obtusatum Sullivant in Sullivant & Wormley: I, [G.C. 4806a], 1859, (164).
obtusatum Sullivant in Sullivant & Wormley: I, [G.C. 4806b], 1859, (164).
obtusatum Sullivant in Sullivant & Wormley: I, [G.C. 45952], 1859, (164).
salinarum var. *boyeri* (Keeley) Reimer in Patrick & Reimer: L, [Boy. M-VII-19], 1966, (120), {as: *Pleurosigma boyeri* Keeley, 1925, (73)}, **Tfr.**: & **Design.**: Reimer in Patrick & Reimer, 1966, (120).

Protokeelia

hottingeri Reimer & Lee: H, [G.C. 38084], 1984, (146).

Protoraphis

atlantica Gibson: H, [G.C. 53761], 1979, (44).

Pseudoguinardia

recta von Stosch: I, [G.C. 40098], 1985, (176).

Rhaphoneis

fragilaroidea Patrick: H, [G.C. 2296], 1944, (108).
granulata Patrick: H, [G.C. 2296], 1944, (108).
mica Hohn & Hellerman: H, [G.C. 44907], 1966, (61).
psammicola Riznyk: H, [G.C. 62633], 1973, (149).

Rhizosolenia

phuketensis Sundström: I, [G.C. 40101], 1980, (165).
shrubsolii Cleve: I, [G.C. 92030], 1881, (20).
twistata Whiting & Schrader: H, [G.C. 63777], 1985, (180).
twistata Whiting & Schrader: P, [G.C. 63777], 1985, (180).

Scoliopleura

peisonis var. *cuneata* Bahls: I, [G.C. 63090], 1982, (7).

Stauroneis

anceps var. *americana* Reimer: H, [G.C. 44254a], 1961, (141).
anceps var. *americana* Reimer: I, [G.C. 44254b], 1961, (141).
anceps var. *arctica* Patrick & Freese: H, [G.C. 8241a], 1961, (119).
anceps var. *arctica* Patrick & Freese: I, [G.C. 8241b], 1961, (119).
anceps var. *arctica* Patrick & Freese: I, [G.C. 8241c], 1961, (119).
attenuirostris Patrick & Freese: I, [G.C. 8283a], 1961, (119).
attenuirostris Patrick & Freese: H, [G.C. 8283b], 1961, (119).
barrowiana Patrick & Freese: H, [G.C. 8166a], 1961, (119).
barrowiana Patrick & Freese: I, [G.C. 8166b], 1961, (119).
cohnii Hilse in Rabenhorst: I, [G.C. 10436], 1860, (130).
fluminea Patrick & Freese var. *fluminea*: H, [G.C. 8193], 1961, (119).
fusiformis Lohman & Andrews: I, [G.C. 63058], 1968, (90).
hannae Patrick & Freese: I, [G.C. 8244a], 1961, (119).
hannae Patrick & Freese: H, [G.C. 8244b], 1961, (119).
hercynica var. *major* Patrick & Freese: I, [G.C. 8262a], 1961, (119).
hercynica var. *major* Patrick & Freese: H, [G.C. 8262b], 1961, (119).
livingstonii Reimer: H, [G.C. 44272a], 1961, (141).
livingstonii Reimer: I, [G.C. 44272b], 1961, (141).
nana Lohman & Andrews: I, [G.C. 63058], 1968, (90).
salsa var. *elliptica* Patrick & Freese: H, [G.C. 8260], 1961, (119).
salsa Patrick & Freese var. *salsa*: H, [G.C. 8189a], 1961, (119).
salsa Patrick & Freese var. *salsa*: I, [G.C. 8189b], 1961, (119).
salsa Patrick & Freese var. *salsa*: I, [G.C. 8189c], 1961, (119).
smithii var. *minima* Haworth: I, [G.C. 13699], 1974, (53).
staurolineata Reimer: H, [H.L.Sm.EX 502], 1961, (141).
undulata Hilse in Rabenhorst: I, [G.C. 11276], 1860, (130).
undulata Hilse in Rabenhorst: I, [G.C. 13059], 1860, (130).

Stauroneis (continued)

vesca Lohman & Andrews: I, [G.C. 63058], 1968, (90).

Stephanodiscus

invisitatus Hohn & Hellerman: H, [G.C. 7059a], 1963, (60).
invisitatus Hohn & Hellerman: I, [G.C. 7059b], 1963, (60).
invisitatus Hohn & Hellerman: I, [G.C. 55024a], 1963, (60).
invisitatus Hohn & Hellerman: I, [G.C. 55024b], 1963, (60).
superiorensis Stoermer & Theriot in Theriot & Stoermer: H, [G.C. 53949], 1984, (171).
yellowstonensis Theriot & Stoermer: H, [G.C. 63257], 1984, (171).

Striatella

hustedtiana Patrick: H, [G.C. 26618a], 1970, (117).
hustedtiana Patrick: I, [G.C. 26618b], 1970, (117).
hustedtiana Patrick: I, [G.C. 26618c], 1970, (117).
hustedtiana Patrick: I, [G.C. 26618d], 1970, (117).

Surirella

acredula Hohn & Hellerman: H, [G.C. 44460], 1963, (60).
adumbratus Hohn & Hellerman: H, [G.C. 44257a], 1963, (60).
adumbratus Hohn & Hellerman: I, [G.C. 44257b], 1963, (60).
adumbratus Hohn & Hellerman: I, [G.C. 44257c], 1963, (60).
agmatilis Camburn in Camburn, Lowe and Stoneburner: H, [G.C. 53758], 1978, (18).
alicula Hohn & Hellerman: H, [G.C. 44458], 1963, (60).
barca Hohn & Hellerman: H, [G.C. 44468], 1963, (60).
brasiliensis Patrick: H, [G.C. 25736], 1944, (109).
carolinicola Camburn in Camburn, Lowe and Stoneburner: H, [G.C. 53757], 1978, (18).
carolinicola Camburn in Camburn, Lowe and Stoneburner: I, [G.C. 54140], 1978, (18).
iowensis Lowe: I, [G.C. 52647], 1972, (91).
margaretiana Patrick & Freese: H, [G.C. 8182], 1961, (119).
melosiroides Meneghini (in litt.) ex Kützing: I, [G.C. 13664], 1844, (81).
ovulum var. *hyalina* Patrick & Freese: H, [G.C. 8248a], 1961, (119).
ovulum var. *hyalina* Patrick & Freese: I, [G.C. 8248b], 1961, (119).
salaria Patrick & Freese: I, [G.C. 8283a], 1961, (119).
salaria Patrick & Freese: H, [G.C. 8283b], 1961, (119).
stalagma Hohn & Hellerman: H, [G.C. 44471], 1963, (60).
stiria Hohn & Hellerman: H, [G.C. 44902], 1966, (61).
stoermeri Lowe: I, [G.C. 52648], 1972, (91).
striatula var. *spinifera* Hohn & Hellerman: H, [G.C. 8099a], 1966, (61).
striatula var. *spinifera* Hohn & Hellerman: I, [G.C. 8099b], 1966, (61).

Surirella (continued)

terryi var. *arctica* Patrick & Freese: I, [G.C. 8225a], 1961, (119).
terryi var. *arctica* Patrick & Freese: H, [G.C. 8225b], 1961, (119).

Synedra

acus var. *varipunctata* John: H, [G.C. 40092], 1981, (70).
alaskana Patrick & Freese: H, [G.C. 8259a], 1961, (119).
alaskana Patrick & Freese: I, [G.C. 8259b], 1961, (119).
barrowiana Patrick & Freese: I, [G.C. 8159a], 1961, (119).
barrowiana Patrick & Freese: I, [G.C. 8159b], 1961, (119).
barrowiana Patrick & Freese: I, [G.C. 8159c], 1961, (119).
barrowiana Patrick & Freese: I, [G.C. 8159d], 1961, (119).
barrowiana Patrick & Freese: H, [G.C. 8159e], 1961, (119).
cyclopum var. *gibbosa* Moghadam: H, [G.C. 62293a], 1969, (99).
cyclopum var. *gibbosa* Moghadam: I, [G.C. 62293b], 1969, (99).
cyclopum var. *incisa* Cunningham in Cunningham & Whitson: I, [G.C. 64379], 1978, (29).
cyclopum var. *incisa* Cunningham in Cunningham & Whitson: H, [ILL LCu.-1 I], 1978, (29).
cyclopum var. *incisa* Cunningham in Cunningham & Whitson: P, [ILL LCu.-2 I], 1978, (29).
cyclopum var. *incisa* Cunningham in Cunningham & Whitson: P, [ILL LCu.-3 I], 1978, (29).
cyclopum var. *incisa* Cunningham in Cunningham & Whitson: P, [ILL LCu.-4 I], 1978, (29).
delicatissima Wm. Smith var. *delicatissima*: L, [Wm.Smith 147], 1853, (161), **Design.:** Patrick in Patrick & Reimer, 1966, (120).
homostriata Hohn: H, [G.C. 44474], 1961, (57).
incisa Boyer: L, [Boy. A-VI-5], 1920, (14), **Design.:** Patrick in Patrick & Reimer, 1966, (120).
isabelae Patrick var. *isabelae*: H, [G.C. 26618a], 1970, (117).
isabelae Patrick var. *isabelae*: I, [G.C. 26618b], 1970, (117).
isabelae Patrick var. *isabelae*: I, [G.C. 26618c], 1970, (117).
isabelae Patrick var. *isabelae*: I, [G.C. 26618d], 1970, (117).
isabelae var. *minor* Patrick: H, [G.C. 26624a], 1970, (117).
lismorensis Playfair: I*, [G.C. 40023a], 1915, (122).
lismorensis Playfair: I*, [G.C. 40024a], 1915, (122).
lismorensis Playfair: I*, [G.C. 40025a], 1915, (122).
lismorensis Playfair: I*, [G.C. 40026a], 1915, (122).
netronoides Hohn & Hellerman: H, [G.C. 44452], 1963, (60).
palea Kützing var. *palea*: I*, [G.C. 3035], 1844, (81).
phantasma Hohn: H, [G.C. 25861a], 1966, (58).
planktonica Hains & Sebring: H, [G.C. 53763], 1981, (48).
recava Hohn: H, [G.C. 44474], 1961, (57).
ridica Hohn & Hellerman: H, [G.C. 6527a], 1966, (61).
ridica Hohn & Hellerman: I, [G.C. 6527b], 1966, (61).

Synedra (continued)

rumpens var. *fusa* Patrick: I, [G.C. 25079], 1941, (106).
rumpens var. *fusa* Patrick: I, [G.C. 25308], 1941, (106).
rumpens var. *fusa* Patrick: H, [G.C. 25422a], 1941, (106).
scina Hohn & Hellerman: H, [G.C. 44902], 1966, (61).
socia Wallace: H, [G.C. 4036a], 1960, (178).
socia Wallace: I, [G.C. 4036b], 1960, (178).
stela Hohn & Hellerman: H, [G.C. 44452], 1963, (60).

Tabellaria

flocculosa var. *linearis* Koppen: H, [G.C. 62833], 1975, (77).
flocculosa var. *linearis* Koppen: P, [G.C. 62834], 1975, (77).
quadriseptata Knudson: I, [G.C. 13672a], 1952, (74).
quadriseptata Knudson: I, [G.C. 13672b], 1952, (74).
quadriseptata Knudson: I, [G.C. 13672c], 1952, (74).
quadriseptata Knudson: I, [G.C. 13786], 1952, (74).
quadriseptata Knudson: I, [G.C. 13787], 1952, (74).
quadriseptata Knudson: I, [G.C. 13788], 1952, (74).

Thalassiosira

frenguelliopsis Fryxell & Johansen in Johansen & Fryxell: I, [G.C. 92035], 1985, (66).
maculata Fryxell & Johansen in Johansen & Fryxell: P, [G.C. 92036], 1985, (66).
multipora Whiting & Schrader: P, [G.C. 63778], 1985, (180).
multipora Whiting & Schrader: H, [G.C. 63778], 1985, (180).
nordenskioldi Cleve var. *nordenskioldi*: I*, [G.C. 92004], 1873, (19).
solitaria Gayoso: I, [G.C. 55091a], 1985, (43).
solitaria Gayoso: I, [G.C. 55091b], 1985, (43).

Triceratium

sinense Schwarz in Rabenhorst: I, [G.C. 35156], 1874, (137).

Vanheurckia

rhomboides var. *neglecta* f. *minor* Playfair: I*, [G.C. 40027a], 1915, (122).

LITERATURE CITED

1. AGARDH, C. A. 1827. Flora oder Botanische Zeitung 2(40), 28 Oct. 1827: 625-640.
2. AGARDH, C. A. 1831. Conspectus Criticus Diatomacearum. Lund. pt. 3, pp. 33-48.
3. ANDREWS, G. W. 1966. Late Pleistocene diatoms from the Trempealeau Valley, Wisconsin. Contr. Paleont., Geol. Surv. Prof. Paper 523-A. 27 pp., 3 pl.
4. ANDREWS, G. W. 1970. Late Miocene nonmarine diatoms from the Kilgore area, Cherry County, Nebraska. Contr. Paleont., Geol. Surv. Prof. Paper 683-A. 24 pp., 3 pl.
5. ANDREWS, G. W. 1971. Early Miocene nonmarine diatoms from the Pine Ridge area, Sioux County, Nebraska. Contr. Paleont., Geol. Surv. Prof. Paper 683-E. 17 pp., 2 pl.
6. BAHLS, L. L. 1981. Diatoms of Lewis and Clark Caverns. Proc. Montana Acad. Sci. 40: 11-18.
7. BAHLS, L. L. 1982. Eight new diatom genus records for Montana. Proc. Montana Acad. Sci. 41: 79-86.
8. BAHLS, L. L. 1983. A new diatom from southeastern Montana. Proc. Montana Acad. Sci. 42: 1-6.
9. BAILEY, L. W. 1861. Notes on new species of microscopical organisms, chiefly from the Para River, South America. Boston J. Nat. Hist. 7(3): 329-351, pl. 7-8.
10. BOURRELLY, P. AND E. MANGUIN. 1954. Contribution a la flore algale d'eau douce des Iles Kerguelen. Mém. Inst. Scient. Madagascar, Sér. B, 5: 7-58.
11. BOYER, C. S. 1914. A new diatom. Proc. Acad. Nat. Sci. Philadelphia 66: 219-221.
12. BOYER, C. S. 1916. Diatomaceae of Philadelphia and vicinity. J. B. Lippincott, Philadelphia. 143 pp., 40 pl.
13. BOYER, C. S. 1920. Rare species of North American Diatomaceae. Bull. Torrey Bot. Club 47: 67-72, 2 pl.
14. BOYER, C. S. 1922. New and rare species of Diatomaceae. Contr. Biol. and Micr. Sect. Acad. Nat. Sci. Philadelphia 1: 1-17.
15. BOYER, C. S. 1927. Synopsis of North American Diatomaceae. I. Coscinodiscatae, Rhizosolenatae, Biddulphiatae, Fragilariatae. Proc. Acad. Nat. Sci. Philadelphia suppl. 78: 3-228.
16. CAMBURN, K. E. AND J. C. KINGSTON. 1986. The genus *Melosira* from soft-water lakes with special reference to northern Michigan, Wisconsin and Minnesota. *In:* Diatoms and lake acidity. Smol, Battarbee, Davis and Meriälainen eds., W. Junk, Dortrecht. pp. 17-34.
17. CAMBURN, K. E. AND R. L. LOWE. 1978. *Achnanthes subrostrata* var. *appalachiana* Camburn and Lowe var. nov., a new diatom from the Southern Appalachian Mountains. Castanea 43: 247-255.
18. CAMBURN, K. E., R. L. LOWE AND D. L. STONEBURNER. 1978. The haptobenthic diatom flora of Long Branch Creek, South Carolina. Nova Hedw. 30: 149-279.
19. CLEVE, P. T. 1873. On diatoms from the Arctic Sea. Bih. K. Svenska Vet.-Akad. Handl. 1(13): 1-29, 4 pl.
20. CLEVE, P. T. 1881. On some new and little known diatoms. K. Svenska Vet.-Akad. Handl. 18(5): 1-28, 6 pl.
21. CLEVE, P. T. 1891. The Diatoms of Finland. Acta Soc. Fauna Fl. Fennica 8(2): 1-68, 3 pl.
22. CLEVE, P. T. 1892. Sur quelques nouvelles formes du genre *Mastogloia*. Le Diatomiste 1(11): 159-163, pl. 23.
23. CLEVE, P. T. 1893. Sur quelques espèces nouvelles ou peu connues. Le Diatomiste 2(13): 12-16, pl. 1.
24. CLEVE, P. T. 1894. Synopsis of the naviculoid diatoms. K. Svenska Vet.-Akad. Handl., Ny Följd 26(2): 1-194, 5 pl.
25. CLEVE, P. T. 1896. Synopsis of the naviculoid diatoms. K. Svenska Vet.-Akad. Handl., Ny Följd 27(3): 1-220, 4 pl.
26. CLEVE, P. T. AND A. GRUNOW. 1880. Beiträge zur Kenntniss der arctischen Diatomeen. K. Svenska Vet.-Akad. Handl. 17(2): 1-121, 7 pl.
27. CLEVE, P. T. AND J. D. MÖLLER. 1878. Diatoms. Exsiccata 49-108, Upsala.
28. CLEVE, P. T. AND J. D. MÖLLER. 1878. Diatoms. Exsiccata 109-168, Upsala.
29. CUNNINGHAM, G. A. AND P. D. WHITSON. 1978. Quantitative character analysis for a new variety of *Synedra cyclopum* (Bacillariophyceae). J. Phycol. 14: 526-529.
30. CZARNECKI, D. B. AND D. W. BLINN. 1978. Observations on southwestern diatoms. I. *Plagiotropis arizonica* n. sp. (Bacillariophyta, Entomoneidaceae), a large mesohalobous diatom. Trans. American Micr. Soc. 97(3): 393-396.
31. CZARNECKI, D. B. AND D. W. BLINN. 1979. Observations on southwestern diatoms. II. *Caloneis latiuscula* var. *reimeri* n. var., *Cyclotella pseudo stelligera* f. *parva* n. f. and *Gomphonema mon-*

tezumense n. sp., new taxa from Montezuma Well national monument. Trans. American Micr. Soc. 98(1): 110-114.

32. Ehrenberg, C. G. 1837. Über ein aus fossilen Infusorien bestehendes, 1832 zu Brod verbacknes Bergmehl von den Grenzen Lapplands in Schweden. Ber. Akad. Wiss. Berlin for 1837: 43-45.
33. Ehrenberg, C. G. 1843. Verbreitung und Einfluss des mikroskopischen Lebens in Süd- und Nord-Amerika. Phys. Abh. Akad. Wiss. Berlin for 1841: 291-445, 4 pl.
34. Ehrenberg, C. G. 1854. Mikrogeologie. Das Erden und Felsen schaffende wirken das unsichtbar kleinen selbständigen Lebens auf der Erde. Leopold Voss, Leipzig. Text 374 pp., Atlas 40 pl.
35. Fiorini-Mazzanti, E. 1856. Sopra una nuova diatomea. Atti Accad. Pontif. Nuov. Lincei Dec. 1856: 1-2, 1 pl.
36. Foged, N. 1952. Diatoms in trumpet-formed catching-nets of *Neureclipsis bimaculata* L. in Sweden. Bot. Not. 2: 157-184.
37. Foged, N. 1955. Diatoms from Peary Land, North Greenland collected by Kjeld Holmen. Medd. om Grønland, Komm. Vidensk. Undersøg. Grønland 128(7): 1-90, 14 pl.
38. Foged, N. 1958. The diatoms in the basalt area and adjoining areas of Archean rock in West Greenland. Medd. om Grønland, Komm. Vidensk. Undersøg. Grønland 156(4): 1-146, 16 pl.
39. Foged, N. 1964. Freshwater diatoms from Spitsbergen. Tromsø Museums Skrifter 11: 1-205, 22 pl.
40. Fuge, P. D. 1937. *Nitzschia firthii* spec. nov., a diatom from Chinese canned fish. J. Royal Micr. Soc. ser. 3, 57: 183-185.
41. Fusey, P. 1950. Contribution a la flore algologique du Jura. II Diatomées des régions de Montbenoit et du Russey (Doubs.). Microscopie 2(3): 149-164.
42. Fusey, P. 1951. Contribution a la flore algologique de Bretagne, Diatomées de la région de Corlay (Côtes-du-Nord). Microscopie, ser. 2, 1(2): 31-50.
43. Gayoso, A. M. 1985. *Thalassiosira solitaria* sp. nov., from Narragansett Bay. Bot. Mar. 28: 477-484.
44. Gibson, R. A. 1979. *Protoraphis atlantica* sp. nov., a new marine epizoic diatom. Bacillaria 2: 109-126.
45. Gregory, W. 1856. Notice of some new species of British fresh-water diatomaceae. Quart. J. Micr. Sci. 4: 1-14, 1 pl.
46. Greville, R. K. 1855. Report on a collection of diatomaceae made in the district of Braemar by Professor Balfour and Mr. George Lawson. Ann. Mag. Nat. Hist., Ser. 2, 15: 252-261, 9 pl.
47. Grunow, A. 1865. Ueber die von Herrn Gerstenberger in Rabenhorst's Decaden ausgegebenen Süsswasser-Diatomeen und Desmidiacean von der Insel Banka, nebst untersuchungen über die Gattung *Ceratoneis* und *Frustulia*. *In:* L. Rabenhorst, Beiträge zur näheren Kenntniss und Verbreitung der Algen, Heft 2: 1-16, pl. 1-2.
48. Hains, J. J. Jr. and M. M. Sebring. 1981. Description and distribution of *Synedra planktonica* n. sp. (Bacillariophyceae). Trans. American Micr. Soc. 100(2): 159-164.
49. Hart, T. J. 1935. On the diatoms of the skin film of whales, and their possible bearing on problems of whale movements. Discovery Reports 10: 247-282, pl. 11.
50. Hasle, G. R. and B. C. Booth. 1984. *Nitzschia cylindroformis* sp. nov., a common and abundant nano-plankton diatom of the eastern subarctic pacific. J. Plank. Res. 6(3): 493-503.
51. Hasle, G. R., H. A. von Stosch and E. E. Syvertsen. 1983. Cymatosiraceae, a new diatom family. Bacillaria 6: 9-156.
52. Hauck, F. and P. G. Richter. 1887. Phykotheca Universalis, Sammlung geterockneter Algen sämtlicher Ordnungen und aller Gebiete. Kummer, Leipzig. Fascicle 3.
53. Haworth, E. Y. 1974. Some problems of diatom taxonomy in Scottish lake sediments. British Phycol. J. 9: 47-55.
54. Héribaud, J. 1893. Les Diatomées D'Auvergne. Pensionnat Clermont-Ferrand. 255 pp., 6 pl.
55. Hilse, L. 1860 Beiträge zur Algen - und Diatomaceen - Kunde Schlesiens, insbesondere Strehlens. Jahres - Ber. Schlesischen Ges. Vaterl. Kult. 38: 75-86.
56. Hohn, M. H. 1952. Contributions to the diatoms of western New York state. Trans. American Micr. Soc. 71(3): 270-271.
57. Hohn, M. H. 1961. The relationship between species diversity and population density in diatom populations from Silver Springs, Florida. Trans. American Micr. Soc. 80(2): 140-165.

58. Hohn, M. H. 1966. The Catherwood Foundation Peruvian-Amazon Expedition, XVII- Bacillariophyta. Monograph 14, pp. 459-495. Acad. Nat. Sci. Phila.
59. Hohn, M. H. and J. Hellerman. 1961. The diatoms. *In:* Paleoecology of the Llano Estacado; Publ. #1. Mus. New Mexico Press, Santa Fe, New Mexico. pp. 98-104.
60. Hohn, M. H. and J. Hellerman. 1963. The taxonomy and structure of diatom populations from three eastern North American rivers using three sampling methods. Trans. American Micr. Soc. 82(3): 250-329.
61. Hohn, M. H. and J. Hellerman. 1966. New diatoms from the Lewes- Rehoboth Canal, Delaware and Chesapeake Bay area of Baltimore, Maryland. Trans. American Micr. Soc. 85(1): 115-130.
62. Holmes, R. W. 1985. The morphology of diatoms epizoic on Cetaceans and their transfer from *Cocconeis* to two new genera, *Bennettella*, and *Epipellis*. British Phycol. J. 20(1): 43-57.
63. Hustedt, F. 1930. Bacillariophyta (Diatomeae) *In:* Die Süsswasser-Flora Mitteleuropas. Herausgegeben von Prof. Dr. A. Pascher, Heft 10, Gustav Fischer, Jena. 466 pp.
64. Hustedt, F. 1931. Die Kieselalgen *In:* Dr. L. Rabenhorst's Kryptogamen-Flora von Deutschland, Österreich und der Schweiz, 7(2)(1).
65. Hustedt, F. 1932. Die Kieselalgen *In:* Dr. L. Rabenhorst's Kryptogamen-Flora von Deutschland, Österreich und der Schweiz, 7(2)(2).
66. Johansen, J. R. and G. A. Fryxell. 1985. The genus *Thalassiosira* (Bacillariophyceae): studies on species occurring south of the Antarctic Convergence Zone. Phycologia 24(2): 155-179.
67. John, J. 1980. Two new species of the diatom *Mastogloia* from Western Australia. Nova Hedw. 33: 849-858.
68. John, J. 1981. Three new taxa of diatoms from Western Australia. Cryptogamie, Algologie II 2: 131-139.
69. John, J. 1981. *Amphora australiensis* sp. nov. Nova Hedw. 35: 39-53.
70. John, J. 1981. New species of freshwater diatoms from Western Australia. Nova Hedw. 34: 569-576.
71. John, J. 1982. Observations on *Hyalodiscus lentiginosus* sp. nov. from Western Australia. Nova Hedw. 36: 409-421.
72. Kalinsky, R. G. 1984. Notes on Louisiana diatoms. III. Some new, rare, and interesting diatoms from northwestern Louisiana. *In:* Proc. VII Int. Diat. Symp., D.G. Mann ed., pp. 299-306.
73. Keeley, F. J. 1925. *Pleurosigma boyeri,* a new diatom from Florida. Proc. Acad. Nat. Sci. Philadelphia 77: 31-32.
74. Knudson, B. M. 1952. The diatom genus*Tabellaria* I. Taxonomy and morphology. Ann. Bot. N.S. 16(63): 421-440.
75. Kociolek, J. P. and E. F. Stoermer. 1986. Observations on North American *Gomphoneis* (Bacillariophycae). II. Descriptions and ultrastructure of two new species. Trans. American Micr. Soc. 105(2): 141-151.
76. Koerner, H. 1970. Morphologie und Taxonomie der Diatomeengattung *Asterionella.* Nova Hedw. 20: 557-724.
77. Koppen, J. D. 1975. A morphological and taxonomic consideration of *Tabellaria* (Bacillariophyceae) from the northcentral United States. J. Phycol. 11(2): 236-244.
78. Krasske, G. 1929. Beiträge zur Kenntnis der Diatomeenflora Sachsens. Bot. Archiv. 27: 348-380.
79. Kützing, F. T. 1833. Algarum Aqua Dulcis Germanicarum, C. A. Schwetschkii et fil., Halis, Saxonum. Decas V.
80. Kützing, F. T. 1833. Synopsis diatomacearum oder Versuch einer systematischer Zusammenstellung der Diatomeen. Linnaea 8: 529-620, pl. 13-19. Berlin.
81. Kützing, F. T. 1844 Die Kieselschaligen Bacillarien oder Diatomeen, W. Köhne, Nordhausen. 152 pp., 30 pl.
82. Kützing, F. T. 1846. Kurze Mittheilung über einige kieselschalige Diatomeen. Bot. Zeit. 4(13): 247-248.
83. Kützing, F. T. 1849. Species Algarum. F.A. Brockhaus, Lipsiae. 922 pp.
84. Lagerstedt, N. G. W. 1873. Sötvattens-diatomaceer från Spetsbergen och Beeren Eiland. Bih. Svenska Vet.-Akad. Handl. 1(14): 1-52, 2 pl.
85. Lamouroux, J. V. F., J. B. G. M. Bory de Saint-Vincent and J. A. Deslonochamps. 1824. Encyclopédie Méthodique. Agasse, Paris. 819 pp.
86. Lee, J. J., C. W. Reimer and M. E. McEnery. 1980. The identification of diatoms isolated as endosymbionts from larger foraminifera from the

Gulf of Eilat (Red Sea) and the description of 2 new species, *Fragilaria shiloi* sp. nov. and *Navicula reissii* sp. nov. Bot. Mar. 23: 41-48.

87. Lee, J. J. and C. W. Reimer. 1984. Isolation and identification of endosymbiotic diatoms. *In:* Proc. VII Int. Diatom Symp., 1982, D. G. Mann ed., pp. 327-343.

88. Lewis, F. W. 1864 On some new and singular intermediate forms of diatomaceae. Proc. Acad. Nat. Sci. Philadelphia 15: 336-346.

89. Lewis, F. W. 1865 On extreme and exceptional variation of diatoms, in some White Mountain localities. Proc. Acad. Nat. Sci. Philadelphia 17: 7-18, pl. 1-2.

90. Lohman, K. E. and G. W. Andrews. 1968. Late Eocene nonmarine diatoms from the Beaver Divide area Fremont county, Wyoming. Cont. Paleont., Geol. Surv. Prof. Paper 593-E. 26 pp., 2 pl.

91. Lowe, R. L. 1972. Notes on Iowa diatoms X: New and rare diatoms from Iowa. Proc. Iowa Acad. Sci. 79: 66-69.

92. Lowe, R. L. and J. P. Kociolek. 1984. New and rare diatoms from Great Smoky Mountains National Park. Nova Hedw. 39: 465-476.

93. Maillard, R. 1962 Florule diatomique de la Région d'Evreux. Rev. Algol. N.S., 6(3): 159-161, 2 pl.

94. Mann, A. 1907. Report on the diatoms of the Albatross Voyages in the Pacific Ocean, 1888-1904. Contrib. U.S. Nat. Herb. X, 5, pp. 221-443.

95. Mayer, A. 1917. Beiträge zur Diatomeenflora Bayerns. Denk. Bayr. Bot. Ges. Regensburg 13(7): 1-151.

96. McCall, D. 1933. Diatoms (recent and fossil) of the Tay District. J. Linn. Soc. London 69: 219-308.

97. McIntire, C. D. and C. W. Reimer. 1974. Some marine and brackish-water *Achnanthes* from Yaquina Estuary, Oregon (U.S.A.). Bot. Mar. 17: 164-175.

98. Mills, F. W. 1934. An index to the genera and species of the diatomaceae and their synonyms. Wheldon & Wesley, London. pt. 17, pp. 1241-1320.

99. Moghadam, F. 1969. An ecological and systematic study of the planktonic diatom communities in Flathead Lake, Montana. Proc. Acad. Nat. Sci. Philadelphia 121(6): 153-228.

100. Morrow, A. C., T. R. Deason and D. Clayton. 1981. A new species of the diatom genus *Eunotia.* J. Phycol. 17(3): 265-270.

101. Müller, O. F. 1786. Animalcula Infusoria. Nicolai Möller, Hauniae. 367 pp.

102. Navarro, J. N. 1982. A survey of the marine diatoms of Puerto Rico. IV. Suborder Araphidineae: Families Diatomaceae and Protoraphidaceae. Bot. Mar. 25: 247-263.

103. Østrup, E. 1910. Danske Diatoméer. C. A. Reitzels, Kjøbenhavn. 323 pp., 5 pl.

104. Palmer, T. C. 1910. A new diatom. Proc. Acad. Nat. Sci. Philadelphia 62: 460, pl. 35.

105. Patrick, R. 1940. Some new diatoms from Brazil. Not. Nat. 59, 7 pp.

106. Patrick, R. 1941. Diatoms of northeastern Brazil. Part I, Coscinodiscaceae, Fragilariaceae, and Eunotiaceae. Proc. Acad. Nat. Sci. Philadelphia 92: 191-226.

107. Patrick, R. 1943. The diatoms of Linsley Pond, Connecticut. Proc. Acad. Nat. Sci. Philadelphia 95: 53-110.

108. Patrick, R. 1944. Well-boring at the Brandywine Lighthouse in Delaware Bay. Part II. Miocene diatoms. Not. Nat. 133, 12 pp.

109. Patrick, R. 1944. Estudo limnológico e biológico das lagoas da região litrânea Sul-Riogradense. II. Some new diatoms from the Lagoa dos Quadros. Bol. Mus. Nac. Rio de Janeiro, n.s., Bot., No. 2, 6 pp.

110. Patrick, R. 1945. A taxonomic and ecological study of some diatoms from the Pocono Plateau and adjacent regions. Farlowia 2(2): 143-221.

111. Patrick, R. 1958. Some nomenclatural problems and a new species and a new variety in the genus *Eunotia* (Bacillariophyceae). Not. Nat. 312: 1-15.

112. Patrick, R. 1959. New subgenera and two new species of the genus *Navicula* (Bacillariophyceae). Not. Nat. 324: 1-11.

113. Patrick, R. 1959 New species and nomenclatural changes in the genus *Navicula* (Bacillariophyceae). Proc. Acad. Nat. Sci. Philadelphia 111: 91-108.

114. Patrick, R. 1961. Diatoms (Bacillariophyceae) from the alimentary tract of *Phoenicoparrus jamesii* (Sclater). Postilla 49: 43-56.

115. Patrick, R. 1966. The diatoms. *In:* History of Laguna de Petenxil. Mem. Connecticut Acad. Arts Sci. 17: 74-77.

116. Patrick, R. 1970. The diatoms. *In:* Ianula: An account of the history and development of the Lago di Monterosi, Latium, Italy. Trans. American

Philosophical Soc. 69(4): 112-122.

117. Patrick, R. 1970. The diatom flora of some lakes in the Galapagos Islands. Nova Hedw. (Beih.) 31: 495-510.
118. Patrick, R. 1971. The effects of increasing light and temperature on the structure of diatom communities. Limn. Oceanogr. 16(2): 405-421.
119. Patrick, R. and L. R. Freese. 1961. Diatoms (Bacillariophyceae) from Northern Alaska. Proc. Acad. Nat. Sci. Philadelphia 112: 129-293.
120. Patrick, R. and C. W. Reimer. 1966. The diatoms of the United States exclusive of Alaska and Hawaii. Volume 1. Monographs 13, Acad. Nat. Sci. Philadelphia, Sutter House, Lititz. 688pp.
121. Patrick, R. and C. W. Reimer. 1975. The diatoms of the United States exclusive of Alaska and Hawaii. Volume 2, Part 1. Monographs 13, Acad. Nat. Sci. Philadelphia, Sutter House, Lititz. 213 pp.
122. Playfair, G. I. 1915. Contributions to a knowledge of the biology of the Richmond River. Proc. Linn. Soc. New South Wales for the year 1914. 39(1): 93-151.
123. Playfair, G. I. 1916. Freshwater algae of the Lismore District: with an appendix on the algal fungi and Schizomycetes. Proc. Linn. Soc. New South Wales for the year 1915. 40(2): 310-362.
124. Podzorski, A. C. 1984. *Caponea caribbea* Podzorski a structurally unique new diatom from Jamaica. Nova Hedw. 40: 1-8.
125. Podzorski, A. C. 1985. An illustrated and annotated check-list of diatoms from the Black River waterways, St. Elizabeth, Jamaica. Bibliotheca Diatomologica 7: 1-177.
126. Podzorski, A. C. and H. Håkansson. 1987. Freshwater and marine diatoms from Palawan (a Philippine island). Bibliotheca Diatomologica 13: 1-245.
127. Rabenhorst, L. 1850. Die Algen Sachsens resp. Mittel-Europa's. Dec. 57-58.
128. Rabenhorst, L. 1857. Die Algen Sachsens resp. Mittel-Europa's. Bot. Zeit. 15(14): 243-244.
129. Rabenhorst, L. 1860. Die Algen Sachsens resp. Mittel-Europa's. Dec. 95-96.
130. Rabenhorst, L. 1860. Die Algen Sachsens resp. Mittel-Europa's, Dec. 97-98.
131. Rabenhorst, L. 1861. Die Algen Europa's, Dec. 121-122.
132. Rabenhorst, L. 1862. Die Algen Europa's, Dec. 127-128.
133. Rabenhorst, L. 1862. Die Algen Europa's, Dec. 129-130.
134. Rabenhorst, L. 1865. Die Algen Europa's, Dec. 181-182.
135. Rabenhorst, L. 1871. Diatomaceae exsiccatae totius terrarum orbis. Semicenturia 1 et 2. Dresden.
136. Rabenhorst, L. 1873. Die Algen Europa's, Dec. 236-237.
137. Rabenhorst, L. 1874. Die Algen Europa's, Dec. 240-241.
138. Reichardt, E. 1981. Die Diatomeenflora quelliger und sumpfiger Standorte in der Umgebung von Treuchtlingen. Nova Hedw. 34: 487-519.
139. Reichardt, E. 1983. Diatomeen aus Lough Neagh. Nova Hedw. 38: 411-412.
140. Reimer, C. W. 1959. The diatom genus *Neidium* I. New species, new records, and taxonomic revisions. Proc. Acad. Nat. Sci. Philadelphia 111: 1-35.
141. Reimer, C. W. 1961. New and variable taxa of the diatom genera *Anomoeoneis* Pfitz. and *Stauroneis* Ehr. (Bacillariophyceae) from the United States. Proc. Acad. Nat. Sci. Philadelphia 113: 187-214.
142. Reimer, C. W. 1961. Some aspects of the diatom flora of Cabin Creek Raised Bog, Randolph Co., Indiana. Proc. Indiana Acad. Sci. 71: 305-319.
143. Reimer, C. W. 1966. Consideration of fifteen diatom taxa (Bacillariophyceae) from the Savannah River, including seven described as new. Not. Nat. 397: 1-15.
144. Reimer, C. W. 1970. Some diatoms (Bacillariophyceae) from Cayler Prairie. Nova Hedw. (Beih.) 31: 235-249.
145. Reimer, C. W. 1982 Four unreported diatom (Bacillariophyceae) taxa from northwest Iowa. Nova Hedw. (Beih.) 73: 267-273.
146. Reimer, C. W. and J. J. Lee. 1984. A new pennate diatom: *Protokeelia hottingeri* gen. et sp. nov. Proc. Acad. Nat. Sci. Philadelphia 136: 194-199.
147. Reyes-Vasquez, G. 1970. Studies on the diatom flora living on *Thalassia testudinum* König in Biscayne Bay, Florida. Bull. Mar. Sci. 20(1): 105-134.
148. Rivera R., P., O. Parra B. and M. Gonzalez S. 1973. Fitoplancton del Estero Lenga, Chile. Gayana Inst. Cont. Bot. 23: 1-93.
149. Riznyk, R. Z. 1973. Interstitial diatoms from two tidal flats in Yaquina Estuary, Oregon, U.S.A.

Bot. Mar. 16: 113-138.

150. Ross, R. and P. A. Sims. 1980. *Syringidium* Ehrenb., *Dextradonator* Ross & Sims, nov. gen. and *Abas*. Ross & Sims, nov. gen. Bacillaria 3: 115-127.

151. Rushforth, S. R., I. Kaczmarska and J. Johansen. 1984. The subaerial diatom flora of Thurston Lava Tube, Hawaii. Bacillaria 7: 135-157.

152. Schmidt, A. 1876. Atlas der Diatomaceen-kunde. O. R. Reisland, Leipzig. Ser. 1, Heft 11, pl. 44.

153. Schmidt, A. 1881. Atlas der Diatomaceen-kunde. O. R. Reisland, Leipzig. Ser. 2, Heft 18, pl. 71.

154. Schumann, J. 1864. Preussische Diatomeen. Nachtrag. Schriften der Königlichen Physikalisch-Ökonomischen Gesellschaft zu Königsberg 5: 13-23, pl. 2.

155. Selva, S. B. 1981. Tertiary freshwater diatoms from the Ogallala of western Kansas. Proc. Iowa Acad. Sci. 88(2): 85-90.

156. Sherman, J. W. and R. Patrick. 1981. The waters of Merom: A study of Lake Huleh. 7. Diatom stratigraphy of the 54-M core. Arch. Hydrobiol. 92(2): 199-221.

157. Skuja, H. 1937. Algae. *In*: H. R. E. Handel-Mazzetti Symbolae Sinicae, Bot. Ergebn. Exped. Akad. Wiss. Wien nach Südwest-China 1914-1918, Teil 1, 105 s., 3 taf.

158. Skvortzov, B. V. 1937. Diatoms from Kizaki Lake, Honshu Island, Nippon. Philippine J. Sci. 61: 9-73, 16 pl.

159. Skvortzov, B. V. and K. Meyer. 1928. A contribution to the diatoms of Baikal Lake. Proc. Sungaree River Biol. Sta. 1(5): 1-55, 3 pl.

160. Smith, H. L. 1878. Description of new species of diatoms. American Quart. Micr. J. 1: 12-18, pl. 3.

161. Smith, W. 1853. A synopsis of the British Diatomaceae, Vol. I, John Van Voorst, Paternoster Row, London. 92 pp., 31 pl.

162. Stoermer, E. F. 1963. New taxa and new United States records of the diatom genus *Neidium* from West Lake Okoboji, Iowa. Not. Nat. 358: 1-9.

163. Sullivan, M. J. and C. W. Reimer. 1975. Some diatoms (Bacillariophyceae) from a Delaware salt marsh—four of which are described as new. Bot. Mar. 18: 115-121.

164. Sullivant, W. S. and T. G. Wormley. 1859. On the measurment of the striae of diatoms. American J. Micr. March 1859: 1-4.

165. Sundström, B. G. 1980. *Rhizosolenia phuketensis* sp. nov. and *Rhizosolenia stolterfothii* H. Peragallo (Bacillariophyceae). Bot. Not. 133: 579-583.

166. Tempère, J. and H. Peragallo. 1895. Diatomées du Monde Entier. Ed. 1.

167. Tempère, J. and H. Peragallo. 1908. Diatomées du Monde Entier. Ed. 2.

168. Tempère, J. and H. Peragallo. 1910. Diatomées du Monde Entier. Ed. 2.

169. Theriot, E., H. J. Carney and P. J. Richerson. 1985. Morphology, ecology and systematics of *Cyclotella andina* sp. nov. (Bacillariophyceae) from Lake Titicaca, Peru-Bolivia. Phycologia 24(4): 381-387.

170. Theriot, E. and J. P. Kociolek. 1986. Two new Pliocene species of *Cyclostephanos* (Bacillariophyceae) with comments on the classification of the freshwater Thalassiosiraceae. J. Phycol. 22: 121-128.

171. Theriot, E. and E. Stoermer. 1984. Principal component analysis of *Stephanodiscus*: Observations on two new species from the *Stephanodiscus niagarae* complex. Bacillaria 7: 37-58.

172. Van Landingham, S. L. 1964. Miocene nonmarine diatoms from the Yakima region in south central Washington. Nova Hedw. (Beih.) 14: 1-78, 56 pl.

173. Van Landingham, S. L. 1966. Three new species of *Cymbella* from Mammoth Cave, Kentucky. Int. J. Speleology 2: 133-136.

174. Villareal, T. A. and G. A. Fryxell. 1983. The genus *Actinocyclus* (Bacillariophyceae): Frustule morphology of *A. sagittulus* sp. nov. and two related species. J. Phycol. 19(4): 458-460.

175. von Stosch, H. A. 1980. The two *Lithodesmium* species (Centrales) of European waters. Bacillaria 3: 7-20.

176. von Stosch, H. A. 1985. Some marine diatoms from the Australian region, especially from the Port Phillip Bay and tropical north-eastern Australia. Brunonia 8(2): 293-348.

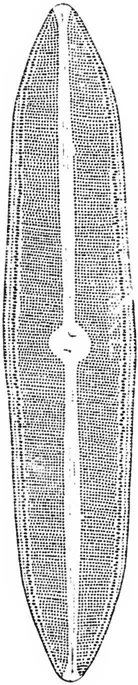
177. von Stosch, H. A. 1987. Some marine diatoms from the Australian region, especially from Port Phillip Bay and tropical north-eastern Australia. II. A survey of the genus *Palmeria* and of the family Lithodesmiaceae including the new genus *Lithodesmioides*. Brunonia 9(1): 29-87.

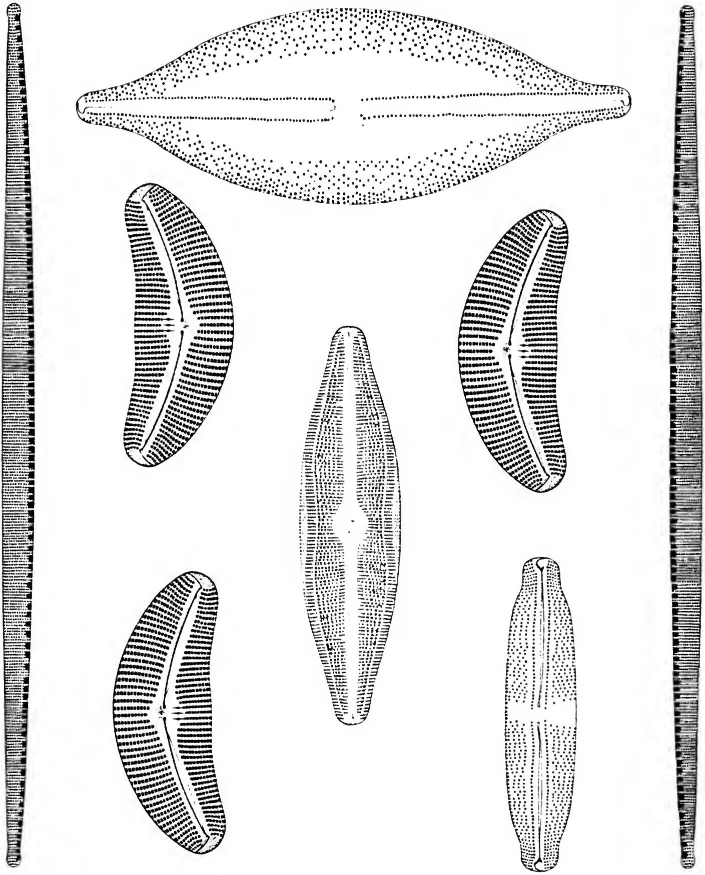
178. Wallace, J. H. 1960. New and variable diatoms. Not. Nat. 331: 1-8.

179. Weber, C. I. 1970. A new freshwater centric

diatom *Microsiphona potomas* gen. et sp. nov. J. Phycol. 6: 149-153.

180. Whiting, M.C. and H. Schrader. 1985. Late Miocene to early Pliocene marine diatom and silicoflagellate floras from the Oregon coast and continental shelf. Micropaleontology 31(3): 249-270.
181. Xie, Shu-qi and Yu-zao Qi. 1984. Light, scanning and transmission electron microscopic studies on the morphology and taxonomy of *Cyclotella shanxiensis* sp. nov. *In:* Proc. VII Int. Diat. Symp., D. G. Mann ed., O. Koeltz, Koenigstein. pp.185-196.
182. Yohn, T. A. and R. A. Gibson. 1981. Marine diatoms of the Bahamas. I. *Mastogloia* Thw. ex Wm. Sm. Species of the groups Lanceolatae and Undulatae. Bot. Mar. 24: 641-655.
183. Yohn, T. A. and R. A. Gibson. 1982. Marine diatoms of the Bahamas. II. *Mastogloia* Thw. ex Wm. Sm. Species of the groups Decussatae and Ellipticae. Bot. Mar. 25: 41-53.





Proceedings of The Academy of Natural Sciences of Philadelphia 139: 307-313, 1987

A New Species of *Phyllagathis* (Melastomataceae) from the Endau-Rompin proposed National Park, Malaysia

BENJAMIN C. STONE
Department of Botany, Academy of Natural Sciences, of Philadelphia
Philadelphia, PA 19103

ANTON WEBER
Institut für Botanik, Universität Wien, Rennweg 14, A 1030 Wien, Austria

ABSTRACT.—*Phyllagathis maxwellii* Stone and Weber sp. nov. (Melastomataceae) is described from the Endau-Rompin proposed National Park in Peninsular Malaysia. Conspicuous and distinctive features include the bullate leaves, inflorescences composed of many-flowered scorpioid cymes, and small cupular fruits. At present the species is known only from the type locality [Endau-Rompin, flowering plants, Malaysia, Melastomaceae, new species, Phyllagathis maxwelli, systematics]

The Endau-Rompin proposed National Park lies in the southeastern part of Peninsular Malaysia, partly in Johore and partly in Pahang, and encompasses about 50,000 hectares on either side of the Sungei (River) Endau. In 1985, the Malayan Nature Society organized a major expedition to investigate the environment, flora and fauna of the area (Kiew 1985, 1986). Endau-Rompin is an area of undulating terrain without high peaks but with rugged topography, and it is still fairly well forested despite the attempt a few years ago to extract timber before the Park could be formally established and the region better known. Endau-Rompin occupies the land between Segamat and Mersing. In terms of world conservation importance, the area is critical because it is the southernmost virgin forest in the Asian continent and one of the very few remaining extensive lowland forest tracts in Peninsular Malaysia. Reports of the M. N. S. expedition are appearing presently. However, collections were made in the area before, and although not separately reported on, references to them may be found in some standard works such as Ridley's flora of the Malay Peninsula (1922-25). A University of Malaya expedition spent a week in the vicinity of Kuala Jasin in 1973. Among the collections made then was the material described here.

Phyllagathis maxwellii Stone & Weber, sp. nov., Figs. 1-4

Herba subprostrata, petiolis elongatis 9-14 cm longis erectis minute hirsuti-setosis, laminis ovatis acuminatis cordatis palmatim 9-11-nervatis, 20 x 12 cm, venis minoribus scalariformibus, supra bullatis, infra ad nervos hirsutulis. Inflorescentia axillaris erecta elongata ad 40 cm longa, interrupte nodosa et breviter ramosa, subscapiformis; ramis floriferis in verticillis brevibus usque ad 3 cm longis, floribus seriatim (secundis) dispositis, pedicellis ad 6-7 mm longis; axibus subhispido-hirsutis, setis ad 1 mm longis, brunneis. Flores c. 6 mm longi, 4-meri, calyce 4 mm lato cupuliformi hispidulo, lobis deltoideis 1 mm longis; petalis asymmetrice obcordatis, apice emarginato et breve cornuto extus; staminibus 8 isomorphicis in alabastro incurvato fil-

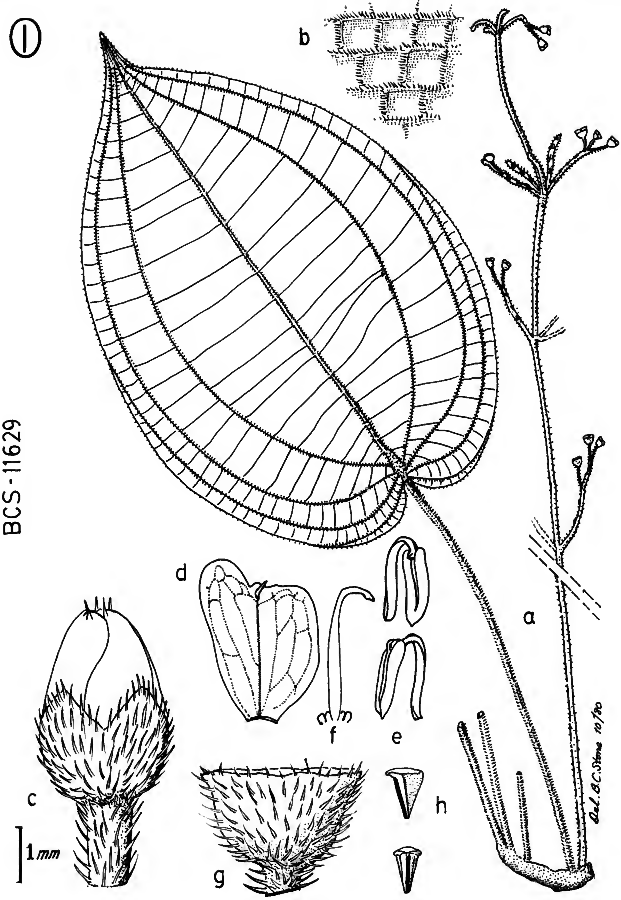


FIG. 1. *Phyllagathis maxwellii* sp. nov. **a**, habit; **b**, and **c**, flower buds; **d**, petal; **e**, stamens; **f**, style; **g**, fruit; **h**, seeds. From type.

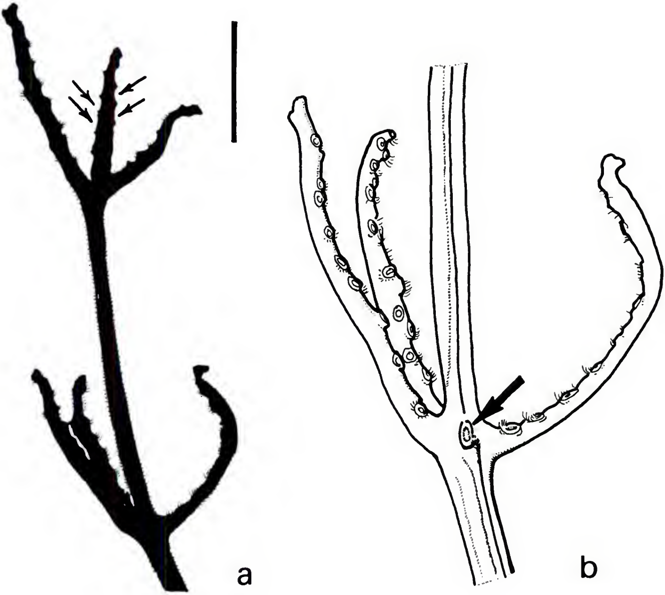


FIG. 2. *Phyllagathis maxwellii* sp. nov. **a**, upper part of inflorescence (flowers and fruit shed). **b**, lower set of cymes, enlarged; note the pedicel scars. Bar = 1 cm.

amento vix 2 mm longo, anthera oblonga c. 1.45 mm longa obtuse brevi-apiculata, connectivo in basi plano vel perminute univerrucato; stylo tenui 2.5 mm longo apice breviter curvato, stigma truncato. Capsula dehiscens, hemiglobosa, truncata, hispidula, seminibus multis cuneiformibus 0.5 mm longis, testa extus cellulis ordinatione interdigitatis (cellulis planiter lobulatis).

TYPE. Peninsular Malaysia, Pahang, Endau-Rompin area, near summit of Bukit Peta on the Johore boundary, 1700 ft alt., in forest over sandstone, 27 Aug 1973, B. C. Stone 11629 (KLU holo, PH iso).

This new species has a strong resemblance to most of the other species of *Phyllagathis* (except *Ph. tuberculata* and its nearest relatives), and in particular is strikingly similar to *Ph. cordata* Ridl., from Gunong Janing, Johore, which has a similar habit and leaf and the erect, almost scape-like inflorescence, but has more numerous, more crowded flowers.

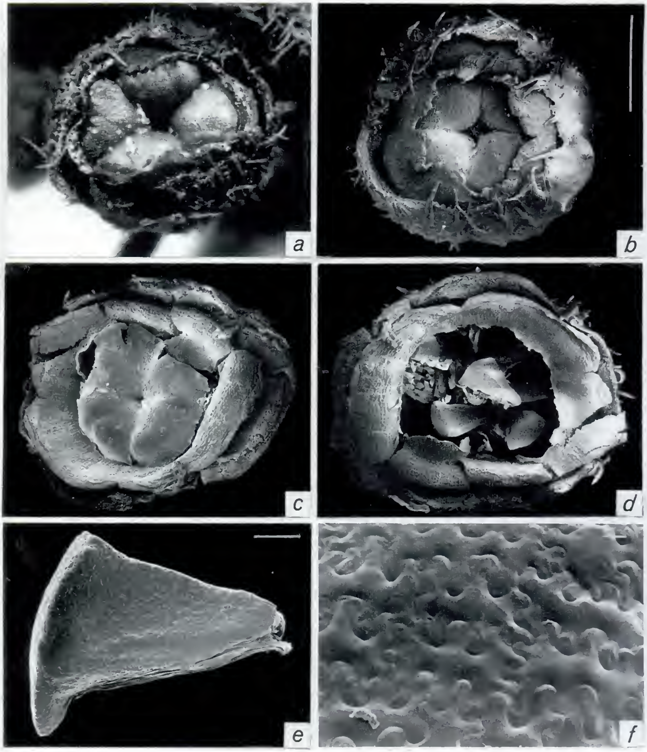


FIG. 3. *Phyllagathis maxwellii* sp. nov. **a, b**, closed fruit; **c**, fruit with spreading limb; **d**, open fruit; **e**; seed; **f**, cell pattern of seed surface; explanation in text. Bar = 1 mm in a-d, 100 µm in e, 10 µm in f. SEM-micrographs (b-f), courtesy Institut für Botanik, Wien.

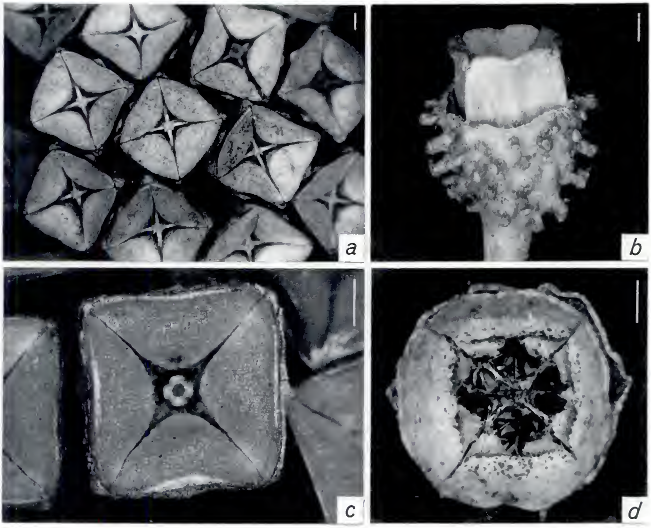


FIG. 4. Fruits of four species of *Phyllagathis* from Malaya. **a**, *Phyllagathis rotundifolia*, top view; **b**, *Phyllagathis scortechinii*, lateral view; **c**, *Phyllagathis stonei*, top view; **d**, *Phyllagathis hispida*, top view. Bar = 1 mm. Photographs by A. Weber.

NOTES ON MORPHOLOGY

In *Phyllagathis maxwellii* the inflorescence is elongate, slender and bears 3 or 4 whorls of usually 4 floriferous branches; subtending bracts are not present. These branches are scorpioid (Fig. 2a, b). Bracteoles are reduced, but their position is marked by a fringe of short bristles. An increase in number of branches (Fig. 1, upper cyme whorl) may be due to initial dichasial branching of the cymes. In fruiting specimens, pedicel-scars show a clearly biseriate arrangement. The fruits, with their pedicels, apparently fall soon after dissemination. The capsules are small, subglobose before dehiscence, with the apex showing 4 bulges (Fig. 3a, b). Between these bulges and the calyx, a ring-like ridge is developed, partly covering the bulges, corresponding to a peripheral excrescence from the ovary. Before dehiscence the ridge spreads to form a round collar around the fruit apex (Fig 3c). Seeds are released thereafter. It seems likely that dissemination is by rain-splash. This form of fruit is very common in the Sonerileae.

The seeds are cuneate (also a common feature in various genera of the Melastomataceae) with a smooth surface consisting of epidermal cells with a lobulate margin (the whole resembling a jig-saw puzzle; Figs. 3e, f).

DISCUSSION

The scorpioid cymes and elongated inflorescence of *Phyllagathis maxwellii* are features also to be found in *Oxyspora* (e.g. *O. wrayi* (King) Maxwell). Ridley removed this species from *Oxyspora* and established a separate genus, *Campimia*, later accepted by Nayar (1975), who added a second species. However, Maxwell (1983) considered these structural features of the inflorescence as not worthy of supporting a generic distinction and *Campimia* a synonym of *Oxyspora*. The same features occuring in *Phyllagathis* support Maxwell's view. Most of the Malayan species of *Phyllagathis* have umbel-like inflorescences (*Ph. rotundifolia*, *Ph. scortechinii*, *Ph. hispida*) or similar but compound umbel-like inflorescences (*Ph. tuberculata*, *Ph. magnifica*, *Ph. stonei*, as described by Weber, 1987). These latter are borne on long stalks. Morphologically these umbel-like structures correspond to complex, contracted thyrses. Three of the Malayan species, including *Ph. maxwellii*, have elongate inflorescences with several flower clusters (*Ph. griffithii*, *Ph. cordata*). The fruits of *Phyllagathis* are generally quadrangular, with four evident scales forming a quadrangular funnel (Fig 4a, c). The seeds are apparently "squeezed" out through the longitudinal slits of the funnel's outer edges (see Weber, 1987).

In *Phyllagathis hispida*, which has fruits quite similar to those of *Ph. maxwellii*, the four ovary scales form a rather rounded, less evidently angular, funnel; there is a distinct platform at the funnel base (a nearly flat fruit apex); and the seeds are released by the disappearance (presumably decay) of this platform, not by being squeezed out through the slits. Thus the fruit functions as a conventional splash-cup. *Ph. hispida*, in respect of its fruits, could be regarded as a link between the 4-angled fruits and the small round capsules of *Phyllagathis maxwellii.*

RELATIONSHIPS

The clearest relationship of *Phyllagathis maxwellii* is to *Ph. cordata*Ridl. which has virtually identical leaves, an elongated inflorescence with short several-flowered side-branches, and a similar habit. However it has a cylindric, glabrous calyx quite different from the rounded, bristly calyx of *Ph. maxwellii*. Moreover, the principal nodes are much closer together, and the lateral branches shorter, with 1-3 flowers. *Ph. cordata* occurs in the region of Gunung Janining, Johore, close to the habitat of *Ph. maxwellii.*

Phyllagathis griffithii is also similar to *Ph. maxwellii*, but differs in having round, glabrous leaves, and a cylindric calyx. It is a widespread species from Malacca north to Perak.

There is an undescribed collection (Davison 21) from Endau-Rompin, obtained on the M. N. S. 1986 expedition, in the Universiti Pertanian herbarium (UPM) which is much like *Ph. maxwellii*, similar in habit (but with long runners present), and similar but somewhat larger fruits. This apparently is yet another species (now under study by Dr Ruth Kiew).

ACKNOWLEGEMENTS

We thank James F. Maxwell (Prince of Songkhla University, Thailand) for his comments and suggestions. The new species is dedicated to him for his important work on several genera of Melastomataceae. Mahmud Sidek, field investigator of the Botany Department, University Malaya, and several Honours students (1973/74) assisted in the collection and processing of specimens.

APPENDIX

List of species of *Phyllagathis* presently known in the Malay Peninsula

1. *Phyllagathis cordata* Ridl.
2. *Ph. griffithii* (Hook. f.) King
3. *Ph. hispida* King
4. *Ph. magnifica* Weber
5. *Ph. maxwellii* Stone & Weber
6. *Ph. rotundifolia* Bl.
7. *Ph. scortechinii* King
8. *Ph. stonei* Weber
9. *Ph. tuberculata* King

LITERATURE CITED

KIEW, B. H. 1985. Endau-Rompin Expedition. Malayan Naturalist 39 (1-2): 6-10.

KIEW, B. H. 1986. Endau-Rompin Expedition. Progress Report June-November 1985. Malayan Naturalist 39 (3-4) : 3-58.

MAXWELL, J. F. 1983. Taxonomic and nomenclatural notes on on *Oxyspora* DC., *Anerincleistus* Korth., *Poikilogyne* Baker f., *Allomorphia* Bl. (Melastomataceae-Oxysporeae). Gardens' Bulletin, Singapore 35 : 109-226.

MAXWELL, J. F. 1986. A synopsis of *Anerincleistus* Korth. and *Oxyspora* DC. (Tribe Oxysporeae, Melastomataceae) in Malay Peninsula. Malayan Nature Journal 37: 217-232.

NAYAR, M. P. 1975. A new combination and notes on the genus *Campimia* Ridl. (Melastomataceae). Bulletin, Botanical Survey of India 14: 188-189.

RIDLEY, H. N. 1922-25. Flora of the Malay Peninsula. 5 vols. L. Reeve and Co., London.

WEBER, A. In press. *Phyllagathis tuberculata* and related new species (Melastomataceae) form Peninsular Malaysia. Plant Systematics and Evolution.

Proceedings of The Academy of Natural Sciences of Philadelphia 139: 315-374, 1987

African Crickets (Gryllidae). 9. New Genera and Species of Brachytrupinae and Gryllinae

DANIEL OTTE
Academy of Natural Sciences, 19th and the Parkway, Philadelphia, PA 19103

ABSTRACT.— This paper concerns the taxonomy of sixty species of Gryllinae and Brachytrupinae belonging to twenty-three genera. Thirty-three species and twelve genera are new. Thirteen incorrectly assigned species are transferred to new or existing genera. A list of all taxa and tranfers is given below. With this paper the preliminary work on African field cricket genera is concluded. [Africa, crickets, Gryllidae, new combinations, new taxa, Orthoptera, songs, systematics]

I have chosen to publish the descriptive work on African crickets in parts. The fauna is so immense, that it will take many years to produce a comprehensive treatment. African collections of crickets have grown rapidly over past few years, and even as this paper was being prepared, much more material has accumulated from recent field work in west Africa. Publishing the work piecemeal allows others to follow the progress of the work and to contribute to the effort much earlier than would be the case if one person held all the relevant material and information in one place.

Much material for which we have no song information has accumulated in various museums, including our own, but, unfortunately, not too much can be done about it until a taxonomy based on songs progresses much further. Eventually we should know enough about the limits of variation and distribution to be able to identify the museum specimens which greater confidence.

Several new genera of forest inhabiting Brachytrupinae (and tentatively assigned to Gymnogryllini) were found in the course of these studies. Some of the species concerned had already been described. In my revisions of *Scapsipedus* and other genera, I encountered the new genus *Mayumbella* from central Africa; the genus *Uluguria*, from the Uluguru Mountains of Tanzania, was found among a collection of specimens in the British Museum; the genus *Taciturna* was discovered in South Africa's eastern evergreen forests; and *Abmisha* was found in the coastal forests of Kenya and Tanzania.

In a previous papers in this series (Otte 1983; Otte, Toms, and Cade in press) we revised what were thought to be two odd members of the Brachytrupinae (*Afrogryllopsis* Randell and *Neogryllopsis* Otte). But in the present paper I argue that these genera belong with Turanogryllus in a separate tribe— the Turanogryllini.

A new genus, *Damaracheta*, belonging to Gryllinae, was first seen in the Academy of Natural Sciences collection. It was later determined to be another specimen of Karny's *Acheta schultzei* (later transferred to *Modicogryllus* by Chopard 1961). Among some specimens sent to me from the South African Museum I found a second species, *capensis*, and, finally, in a recent trip to Malawi I discovered three additional species, *mlozi, kasungu*, and *zomba*.. One of the two *Gryllus* species was found while examining some crickets in the British Museum; the other was tape recorded and collected on the Viphya Plateau in central Malawi. I have also examined the type of *Gryllus subpubescence* Chopard.

Some new species of *Velarifictorus* and one new species of *Modicogryllus* were collected in Malawi in April 1986 by myself, George Glenn, and Jane Ruffin. Two additional *Velarifictorus* from Botswana were sent to me from the University of Pretoria. Songs were recorded for all of the

Malawi species.

The status of the genus *Cophogryllus* is chaotic. Chopard (1967: 37) lists 27 species in the genus ranging from southern Africa to southeast Asia, and one species from Peru. The genus was defined by the complete absence of wings, and many entirely wingless gryllines were placed in the genus without ever examining other features. Since winglessness has evolved many times in the Gryllinae, it is obvious that this genus is presently composed of quite unrelated species, several of which had already been transferred to other genera (Otte and Cade 1983; Otte 1984). The present paper covers eight valid species from southern Africa. Some are previously described taxa which are reexamined for characters previously not described; others are newly collected by myself and R. Toms.

During the course of revising several African genera I encountered a number of species that were misplaced. In some cases they belonged to previously undescribed genera (*Mombasina, Nimbagryllus, Songella, Parasongella,* and *Omogryllus*).

In addition, I have illustrated members of previously poorly defined genera.

Specimens examined are at the following institutions: BERLIN, Zoologisches Museum, Humboldt-Universität; LONDON, British Museum (Natural History); LUND, Zoological Museum; PARIS, Muséum d'Histoire Naturelle; PHILADELPHIA, Academy of Natural Sciences; PRETORIA, Transvaal Museum; STOCKHOLM, Naturhistoriska Riksmuseet; TERVUREN, Musee Royal de l'Afrique Centrale; VIENNA, Naturhistorisches Museum.

LIST OF SPECIES

BRACHYTRUPINAE
  Gymnogryllini
    Abmisha
      illex n. sp.
      sigi n. sp.
    Uluguria n. gen.
      lupanga n. sp.
    Mayumbella n. gen.
      lucens (Chopard) (from *Scapsipedus*)
      atriceps (Chopard) (from *Gryllopsis*)
      luteipennis (Chopard) (from*Gryllopsis*)
    Taciturna new genus
      dlinza n. sp.
      knysna n. sp.

  Turanogryllini
    Turanogryllus Tarbinsky
      niloticus Saussure 1877
      scenicus Randell 1964
      machadoi Chopard 1961
      flavolateralis (Chopard 1934) (from*Gryllopsis*)
      microlyra (Chopard 1938) (from *Gryllopsis*)
      nimba n. sp.
      kitale n. sp.
      sombo n. sp.
      mau n. sp.
    Afrogryllopsis Randell 1964
      charliersi (Chopard 1934)(from *Pologryllus* Karsch)
    Podogryllus
      desultorius Karsch

GRYLLINAE
  Gryllini
    Damaracheta n. gen.
      schultzei (Karny) (from *Modicogryllus*)
      capensis n. sp.
      mlozi n. sp.
      kasungu n. sp.
      zomba n. sp.
    Gryllus Linné
      kapushi n. sp.
      mzimba n. sp.
      subpubescens (Chopard 1934)

  Modicogryllini
    Velarifictorus
      changus n. sp.
      ghanzicus n. sp.
      nyasa n. sp
      dedzai n. sp.
      kasungu n. sp.
      lengwe n. sp.
      viphius n. sp.
    Modicogryllus
      mulanje n. sp.
    Cophogryllus Saussure
      delalandei Saussure 1877
      fasciatus (Walker) 1869 (*Gryllus*)
      maculatus Chopard 1955
      simonsi n. sp.
      eshowensis n. sp.

escourtensis n. sp.
trichardti n. sp.
zoutpansbergi n. sp.
parvipennis Chopard (1963: 340)(moved to *Callo gryllus)*
jeanneli Chopard (1938: 128) *Callogryllus)*
royi Chopard (1954:89 *Modicoides* , Otte & Cade 1984).
camerunensis Chopard (1945:170)(to *Sigagryllus,* Otte 1984).
boromensis Branczik 1897. Status uncertain, type not found.

Mombasina n. gen.
  rufulus (Chopard) (from *Oligachaeta*)
Nimbagryllus n. gen.
  lamottei (Chopard) (from *Gryllopsis*)
Astrupia n. gen.
  gazensis n. sp.
  sodwanensis n. sp.
Cophella n. gen.
  macrocephala n. sp.

Insertae Sedis
Songella n. gen.
  obscuripennis (Chopard) (from *Callogryllus*)
  ebneri (Chopard) (from *Callogryllus*)
Parasongella n. gen.
  nigriceps n. sp.
Callogryllus Sjöstedt
  kilimanjaricus Sjöstedt
  parvus Chopard
  olohius n. sp.
Omogryllus n. gen.
  jeanelli (Chopard) (from *Cophogryllus*)
Oligachaeta Chopard
  chabanaudi (Chopard)
  tripartita (Chopard) (from *Gryllopsis*)
Clearidas Stal
  nigriceps Stal
Grylloderes Bolívar
  testaceus Chopard
  subalatus Chopard

BRACHYTRUPINAE: GYMNOGRYLLINI

ABMISHA n. gen.

TYPE SPECIES. *Abmisha illex* n. sp.

This genus was first seen on a forested slope in the Shimba Hills, near Mombasa, Kenya. Later, a second species was found in the forests along the southern slopes of the East Usambara mountains. Both species were found singing in dense forest in the daytime. Thus far, only the genus *Taciturna* from southern Africa is confined to thick forest in this way; other African members of the subfamily are commonly found in open country or along forest edges. Superficially the genus is very similar to the genus *Velarifictorus* (Gryllinae: Modicogryllini) However, the short front basitarsus (much shorter than the middle basitarsus), the absence of occipital stripes, and the resemblace of the male genitalia to those of *Gymnogryllus* indicate that these species belong to Brachytru-pini rather than to Modicogryllini. The ocelli, however, are not arranged in a straight line as in most Brachytrupinae.

RECOGNITION OF GENUS. Similar in overall appearance to both *Velarifictorus* and *Gymnogryllus*. Distinguished from other Brchytrupinae by male genitalia. Foretibiae with large outer and no inner tympanum. Body color dark brown, but with pale legs and venter. Body length 15-17 mm. Head: dorsum without pale stripes. Pronotum generally dark brown to black; lateral lobes entirely black. Forewings 2.4-3.0 times as long as pronotum. Hindwings hidden, about half as long as pronotum. Foretibiae with only outer tympanum. Hindfemora with broad dark band on outer face (not always distinct. Hind tibiae 0.65-0.70 times as long as hindfemora, with 5 inner and 5 outer subapical spurs.

Abmisha illex n. sp.

TYPE. *Holotype M,* Kenya Shimba Hills, nr. Mombasa, west slope, in forest, 19 ix 1982 (D. Otte 86). PHILADELPHIA.

RECOGNITION. Figs. 2D-J, 4D. Table 1. Differs from *sigi* in shape of genitalia and in being lighter. *Male*: Body color dark brown, but with pale venter and legs; hindfemora with or without two dark bands. Head: dorsum uniformly dark brown (appears black); small median ocellus; ocelli arranged in triangle; face and cheeks uniformly dark brown. Pronotum: with

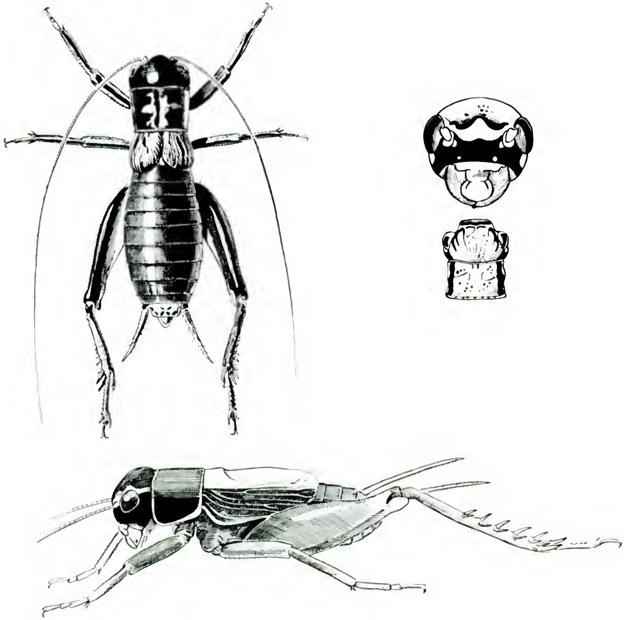


FIG. 1. A, adult male of *Taciturna knysna*; B, *Mayumbella lucens* holotype; C, *Uluguria lupanga*, face and dorsum of head and pronotum.

parallel sides; dark red brown to black, similar to head in color. Forewings: dorsum brown, blackish in apical area; lateral field black. Hindwings: hidden, half as long as pronotum. Abdomen: dorsum dark brown, venter pale. Fore- and midlegs: femora pale but with small dark spots on dorsum, and with large dark patches on inner and especially outer faces at distal end; tibiae dark brown. Hindlegs: femora: outer and upper faces with rows of oblique brown stripes, and with 2 broad dark bands—one at knees and one in middle of femur on upper and outer faces (a paratype male lacks this central band).

HABITAT. Heard singing in the daytime in the forested western slopes of the Shimba Hills in eastern Kenya.

SONG. Fig. 4. Trills with a moderatly slow pulse rate.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratype:* same data as holotype, 1M, PHILADELPHIA.

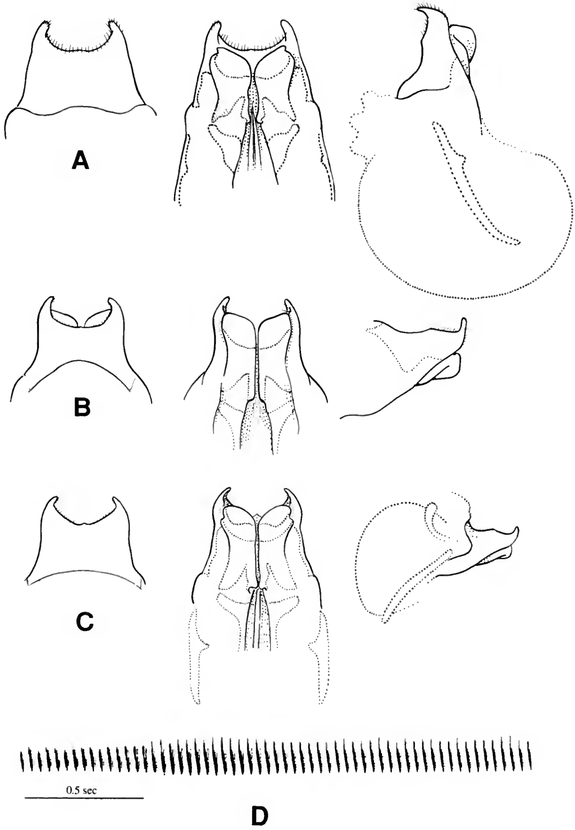


FIG. 2. *Abmisha* male genitalia: dorsal, ventral and lateral views. **A**, *sigi* holotype; **B**, *illex* holotype; **C**, *illex* from type locality. **D**, song of *Abmisha illex* from the Shimba Hills, Kenya.

TABLE 1. Species measurements.

	No. file teeth	BL	FL	CL	FWL/PL	TL/FL	OL/FL	Tymp	sub-apical spurs
Abmisha illex									
HM	99	16	8.8	5.5	2.5	0.65	-	-/O	5/5
PM	106	17	10	7	2.4	0.65	-	-/O	5/5
Abmisha sigi									
HM	113	15.5	9.2	6	2.8	0.69	-	-/O	5/5
Uluguria lupanga									
HM	-	14	9.7	3.5	-	0.55	-	-/-	4/4
PF	-	13	9.7	3.6	-	0.58	-	-/-	4/4
Mayumbella lucens									
LM	190	23	15.3	-	2.6	0.87	-	-/O	5/5
PLF	-	20	16	-	1.24	-	1.2	-/O	5/5
Mayumbella atriceps									
HF	-	19	?	8.5	0.62		?	(15 mm)	-/O
Mayumbella luteipennis									
HF	-	20	13	-	1.57	0.7	0.9	-/O	6/6
Taciturna dlinza									
HM	0	17	10.5	5	0.94	0.54	-	-/-	4/3+1*
PM	0	15	8.9	4.2	1	0.56	-	-/-	4/3+2,3
PM	0	16.5	10.5	5	0.93	-	-	-/-	4/3+1,2
Taciturna knysna									
HM	0	18	9.5	3.7	0.74	0.6	-	-/-	3+2,3 /3+3,5
PM	0	17	9	3.8	0.8	-	-	-/-	3+3/3+3,4
PM	0	16.6	8.7	3.3	0.93	-	-	-/-	3+3/3+3
PM	0	17	8.7	3.5	0.85			-/-	3+3,4/3+5
PF		17	8.2	3.5	0	0.55	-	-/-	3+3/3+2

BL, body length
PL, pronotal length
i, small inner
O, large outer

spines above spurs
CL, cercal length
OL, ovipositor length
I, large inner

Abmisha sigi n. sp.

TYPE. *Holotype M,* Tanzania, East Usambara Mts, Sigi, below Amani, forest, 30 ix 1982 (Otte 103). PHILADELPHIA.

RECOGNITION. Figs. 2A-C, 4E. Table 1. Differs from *illex* in the male genitalia, and in being darker.

Males: Body color dark brown, black on sides of body, pale brown on venter. *Head:* dark reddish brown, nearly black down to mouthparts; orange on mouthparts. *Pronotum:* dorsum dark brown, with pale patch in each posterior quarter, each pale patch with dark central spot; lateral lobes black. *Forewings:* dorsum brown to dark brown; nearly black in apical area; lateral field black. *Hindwings:* hidden, about half as long as pronotum. *Abdomen:* dorsum dark brown; venter brown. *Fore- and midlegs:* femora pale in proximal half, becoming dark brown in distal half; tibiae dark brown. *Hindlegs:* femora with strong dark brown oblique stripes on outer and upper faces, these joining into solid dark brown bands at middle and ends of femora;

HABITAT. Collected in a mountain forest, below Amani in the East Usambara mountains. The area had been quite disturbed by human activities.

SONG. Not known.

SPECIMENS. *Holotype* M, PHILADELPHIA.

ULUGURIA n. gen.

TYPE SPECIES: *Uluguria lupanga* n. sp.

A male and female, of this odd-looking, completely apterous genus, were found in the British Museum of Natural History. The short basal segments of the foretarsi and the configuration of the male genitalia suggest that it is a member of the Brachytrupinae: Gymnogryllini. Nothing is known about its habitat, though we suspect that it is a forest inhabiting crickets.

RECOGNITION OF GENUS. Genitalia as in Fig. 3; wings entirely absent; fore- and midtibiae with only three apical spurs; foretibiae without tympana; head much wider than pronotum, with vertical orientation such that median ocellus is located on front vertical face; forehead very broad and with wide arching pale band across face. See also *U. lupanga* below.

Uluguria lupanga n. sp.

TYPE. *Holotype M,* Tanzania, Uluguru Mts., Lupanga, East, 1600 m, pitfall trap, 10 vii 1981 (Stoltze & Scharff). COPENHAGEN.

RECOGNITION. Figs. 1C, 3G-I. Table 1. *Male*: Body color gray brown on dorsum, with a black band on the side of the body. *Head*: dorsum with faint longitudinal stripes, pubescent; median ocellus nearly obsolete, located on the top of the face; head with a vertical orientation such that the median ocellus is located on a vertical surface. Face with a broad w-shaped pale band below the median ocellus, and with a black band below that which runs below the level of the antennae; clypeus, labrum and mandibles pale brown; cheeks black behind eyes. *Pronotum*: dorsum gray, pubescent, with numerous small dark spots; lateral lobes ivory colored in lower half, black in upper half. *Forewings*: entirly absent. *Thorax and abdomen*: dorsum gray with numerous small dark spots, mostly arranged in transverse rows; mesothoracic segment with two median larger dark spots; fifth tergite with large black spots on either side of tergite. *Forelegs*: Front and middle tarsi with small pearl-colored adhesive pads on venter of first two basal segments; pale brown, basitarsus much shorter than 1/3 length of tibiae; tibiae without auditory tympanum, and with 4 apical spurs; midtibiae pale brown, with 3 apical spurs. *Hindlegs*: femora pale brown with distinct reddish oblique stripes located on outer and upper faces, hind tibiae with 4 inner and 4 outer subapical spurs; dorsal spurs on hind basitarsis almost as large as subapical tibial spurs.

Female: Similar to male in size and color, but side of abdomen less black and more spotted, and fifth tergites without large dark lateral markings as in male.

SPECIMENS. *Holotype M* , COPENHAGEN. *Paratype:* Same data as holotype, 1F, COPENHAGEN.

MAYUMBELLA n. gen.

TYPE SPECIES: *Mayumbella lucens* (Chopard)

The type species of this genus is from Gabon; but we know nothing about its habitats, or song. The placement of this genus under the Brachytrupinae is tentative and is based principally on the shape of the male epiphallus of *M. lucens*, which seems to match more closely with the Brachytrupinae than any other group. Although the females of several other species are here assigned to this genus, much uncertainty remains on this point. It is virtually certain that they do not belong to *Gryllopsis* where Chopard (1967) had placed them.

RECOGNITION OF GENUS. (Based principally upon the lectotype of *M. lucens*). Epiphallus and ectoparameres elogate; body color dark reddish brown; forewing with more than four harp veins; mirror obsolete. Body length 19-23 mm. Body color dark reddish brown. Foretibiae with only outer tympanum. Hindtibiae 0.7-0.87 times as long as hindfemora, and with five or six inner and five or six outer subapical spurs. Ovipositor 0.9-1.2 times as long as hind femur.

Mayumbella lucens (Chopard)

Scapsipedus lucens Chopard 1934: 37. *Lectotype M,* here designated, Gabon, Mayumbe, 5 xi 1913 (R. Verschueren). TERVUREN. Type examined. NEW COMBINATION.

NOTES ON LECTOTYPE. Figs. 1B, 4ABCF. Table 1. Medium to large; body color dark rusty brown on dorsum, blackish on sides. *Head:* as wide as pronotum; dorsum dark reddish brown, without pale stripes; face and cheeks blackish; transition between reddish and black coloration behind eyes sudden; face elongate due to lengthened mouthparts; height of head 3.2 times height of eyes; upper lobe of clypeus narrow, about one half as wide as lower lobe. *Pronotum:* with some pubescence but without bristles; dorsum dark reddish brown like head; lateral lobes black, color transition abrupt. *Forewings:* mirror tiny or obsolete; harp with 6 veins; right forewing irregular venation in chord area, left wing normal; dorsal field dark brown around periphery, somewhat transparent in middle; with pale area on shoulder; lateral field blackish. *Abdomen:* dorsum dark brown, venter reddish brown. *Legs:* All legs reddish brown; foretibiae with only larger outer tympanum; basal tarsomeres of forelegs more than one third as long as femora.

NOTES ON PARALECTOYPE FEMALE. Coloration like male. *Head:* height 3.0 times eye height; narrower than pronotum. *Pronotum:* entirely blackish. *Forewings:* pale, straw-colored on dorsal field, blackish on sides; 1.24 times as long as pronotum; with oblique posterior edges, slightly overlapping medially. Mouthparts not lengthened as in male.

Mayumbella atriceps (Chopard)

Gryllopsis atriceps Chopard 1934: 32. *Holotype M,* Congo [Zaire], Katanga: Lukafu 6-22 1930 (G. F. de Witte). TERVUREN. Type examined. NEW COMBINATION.

The placement of *atriceps* here is uncertain. It is certain that the species does not belong to *Gryllopsis.* The dark brown coloration and the absence of a tympanum on the inner face suggest a relationship to *M. lucens.*

NOTES ON HOLOTYPE. Fig. 4G. Table 1. *Female:* With large head. Body color dark brown on dorsum, pale brown on venter. *Head:* wider than pronotum, blackish but mouth parts reddish brown; lateral ocelli large, median one small; eyes small. *Pronotum:* wider anteriorly; unicolorous dark brown, covered with fine gray pubescence. *Forewings:* hemicircular, slightly overlapping at midline. *Abdomen:* dorsum dark brown but posterior margin of tergites forming pale transverse lines; venter pale brown. *Fore- and midlegs:* dark brown. *Hindlegs:* missing.

Mayumbella luteipennis (Chopard)

Gryllopsis luteipennis Chopard 1934: 31. *Holotype F,* Congo [Zaire], Kinda, 22 v 1914 (L. Charliers). TERVUREN. Type examined. NEW COMBINATION.

The placement of *atriceps* here is uncertain. The dark brown coloration and the absence of a tympanum on the inner face suggest a relationship to *M. lucens.*

NOTES ON HOLOTYPE. Table 1. *Female:* dark brown; dorsum of head blackish; vertex with 6 faint reddish bands; face and cheeks black. *Head*: short (height of head 3.1 times height of eye). Head and pronotum equal in width. *Pronotum:* generally reddish brown, slightly variegated on dorsum, mostly blackish on lateral lobes, but lower anterior corner reddish brown. *Forewings*: small, triangular in dorsal view, not

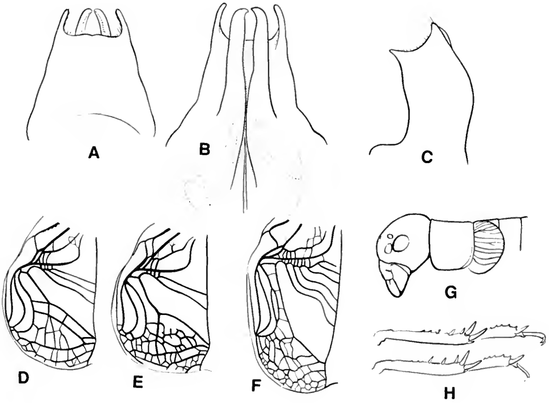


FIG. 3. A-C, male genitalia of *Mayumbella lucens*; **D**, forewing of *Abmisha illex*; E, forewing of *Abmisha sigi*; F, forewing of *Mayumbella lucens*; **G**, *Mayumbella atriceps* female holotype; **H**, *Taciturna knysna*, outer (upper) and inner (lower) views of hind tibiae and tarsi.

overlapping medially (1.57 times as long as pronotum); dorsum straw-colored, lateral field black. *Abdomen:* dark reddish brown, nearly black, but sides of tergum with a row of lighter brown spots (one spot per tergite). *Fore- and midlegs:* black reddish brown; foretibiae with no inner and a large outer tympanum. *Hindfemora:* dark reddish brown, but outer face with darker brown oblique stripes.

TACITURNA n. gen.

TYPE SPECIES: *Taciturna dlinza* n. sp.

We first discovered this genus at oatmeal trails in the Knysna forest. We laid a trail of oatmeal bait along trails in the deep forest and investigated them after dark. Males and females had congregated at the baits and were easily caught. In Zululand another member of the genus was also collected along oatmeal trails, again in deep evergreen cloud forest. These crickets are mute, though they still possess small wingpads, and lack tympanal organs on the foretibiae.

RECOGNITION OF GENUS. Fig. 1. Male epiphallus with long lateral arms (Fig. 6). Male forewings present but without a stridulum. Foretibiae without tympana. Body smooth, shiny red-brown or black. Body length 15-18 mm. Males with small forewings with parallel veins and without a stridulum; forewings shorter than pronotum; females without forewings. Head wider than pronotum. Pronotum much wider in front than in rear. Front legs without tympana. Front basitarsi less than one third the length of the front tibiae. Hind tibiae 0.54-0.60 times as long as hind femur, with 3 or 4 inner and 3 outer subapical spurs and with small spines above the spurs. Cerci short—one-third to half as long as the hind femur.

Taciturna dlinza n. sp.

TYPE. *Holotype M*, South Africa, Natal, Dlinza Forest 30 x 1980 (D. Otte 16). PHILADELPHIA.

RECOGNITION. Fig. 3A-C. Table 1. Distinguished from *knysna* as follows: body color reddish, not black; male epiphallus more slender.

Males: Body color reddish-brown with yellow to orange legs, small forewing pads, without stridulum. *Head:* dorsum uniform reddish-brown; face reddish-brown with yellow inverted U-shaped area ventral to median ocellus, lower half of clypeus whitish, mandibles yellow-orange; cheeks reddish-brown, becoming more pale ventrally. *Pronotum:* dorsum reddish-brown like head; slightly lighter around muscle attachment plates; lateral lobes reddish-brown in upper two-thirds, gradually fading to ivory-colored in lower third; fringe of bristles on posterior and anterior margins reddish in color. *Forewings:* about as long as pronotum, pale brown, with parallel veins, lateral field same as dorsal field in color. *Hindwings*: absent. *Abdomen:* dorsum reddish-brown, tergites becoming ivory-colored on sides; venter pale. *Fore- and midlegs:* Basitarsus on foreleg less than one third as long as foretibiae; femora pale but becoming reddish-brown at distal end; tibiae pale on upper face, then dark brown on lower face. *Hindlegs:* femora yellow orange with reddish oblique stripes; tibiae with 2-3 small spines above orange colored subapical spurs. Hind basitarsus 0.53 times tibial length.

HABITAT. Collected along oatmeal trails laid on leaf litter and ground in a tall natural forest.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratypes*: (PHILADELPHIA) Same place, 12 xi 1980, 2M 1jF. Same place, 30 x 1980, 1M.

Taciturna knysna n. sp.

TYPE. *Holotype M*, South Africa, Cape Province, Garden of Eden, near Knysna, 10 iii 1982 (Otte & Cade 45). PHILADELPHIA.

RECOGNITION. Figs. 1A, 3D-F, 4H. Table 1. Differs from *dlinza* as follows: body color appearing black, hind tibiae with three or more small spines above the subapical spurs; epiphallus not as elongate.

Males: body actually very dark brown, but appearing black; legs black, venter pale brown. *Head:* dorsum black, median ocellus obsolete, lateral ocellus very small, face black ventrad to middle of clypeus, then variegated brown and white on lower lobe of clypeus, labrum brown. *Pronotum:* dorsum narrowing posteriorly, lateral lobes black. *Forewings:* dorsal field black, shorter than pronotum, without stridulum; lateral field black. *Hindwings:* absent. *Abdomen:* dorsum very dark brown; venter pale brown; cerci short, dark brown. *Fore- and midlegs:* dark brown to black. *Hindlegs:* black.

Females: similar to males but without forewings. Ovipositor very short, barely visible.

HABITAT. Deep forest; collected along oatmeal trails laid on forest paths. We colleced mostly males.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratypes*: Same data as holotype, 13M 1F, PHILADELPHIA & PRETORIA.

TURANOGRYLLINI

TYPE GENUS: *Turanogryllus* Tarbinsky.

In the course of my own studies in Australia, the Pacific, and Africa I have come to view the original classification of Saussure 1877 as the one which best describes the relationships among the "field crickets" sensu latu (i.e. among the genera which Chopard (1967) placed under Gryllinae). In the original scheme Saussure placed Gryllus Linné and Brachytrupes Serville into two different groups—the former into Légion Gryllites, and the latter into the Légion

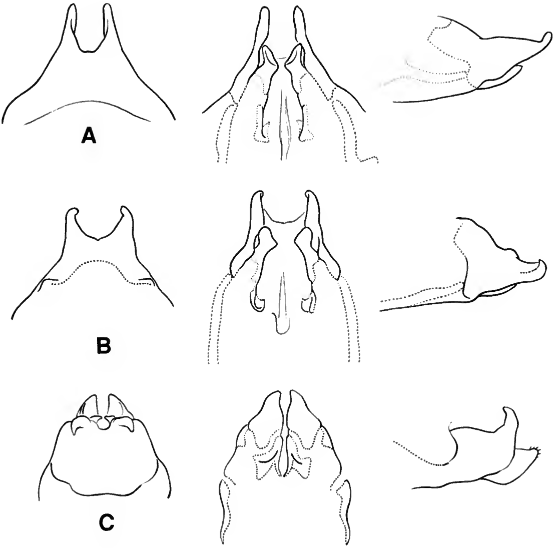


FIG. 4. Male genitalia (dorsal, ventral and lateral views). **A**, *Taciturna dlinza* holotype; **B**, *Taciturna knysna* holotype; **C**, *Uluguria lupanga* holotype.

Brachytrypites—and he called Gymnogryllus and Brachytrupes as subgenera of Brachytrypus. Thus the priority of Brachytrupes over Gymnogryllus as a group name was established. Some confusion occurred, and still exists, in the spelling of the name. Serville's original (1839) name was Brachytrupes, but subsequently various versions of this name were used and applied to the same species (Brachytrypes, Agassiz 1846; Brachytrypus, Saussure 1877; Brachytrypes, Kirby 1906; Brachytrupes, Chopard 1967).

Kirby 1906: 20 also placed *Brachytrupes* together with *Gymnogryllus*, but under the subfamily *Gryllinae B; Gryllus* was placed in *Gryllinae C*. Randell (1964), however, departed radically from this scheme by placing *Brachytrupes* in the tribe Gryllini and *Gymnogryllus* in the tribe Gymnogryllini. This scheme is almost certainly erroneous for it unites *Brachytrupes* with several genera which share few morphological similarities, among them *Loxoblemmus*, *Velarifictorus*, *Modicogryllus*. It was for this reason that Chopard (1967) also separated *Brachytrupes* from *Gymnogryllus*. I have now studied most members of groups which Randell included in Gryllinae:Gymnogryllini (including *Gymnogryllus*, *Turanogryllus*, *Gryllopsis*, *Afrogryllopsis*, *Cophogryllus*, and *Anurogryllus*). On the basis of the male genitalic configuration *Gryllopsis* and *Cophogryllus* belong to Gryllinae: Modicogryllini; *Turanogryllus*, *Afrogryllopsis*, *Neogryllopsis*, and *Podogryllus* belong to Brachytrupinae: Turanogryllini; and *Gymnogryllus* and *Anurogryllus* belong to Brachytrupinae: Gymnogryllini. The characters which define this tribe are given below. The characters which separate the new subfamily Brachytrupinae (equal to Saussure's Légion Brachytripites) are given in a Table 1 below).

RECOGNITION OF TRIBE. Male genitalia large, epiphallus relatively short and the entire structure dominated by huge and sometimes elaborate ectoparameres which form spikes and may have prominent serrations; virga usually stout, though often coming to fine point; endoparamers uniting posteriorly to form large muscle attachment plate. Stridulum with small short setae arranged along both sides of ridge holding file. Foretibiae with small inner tympanum or none at all, but always with large outer tympanum. Harp of male forewings with three or more veins; these veins connected only indirectly to stridulum through series of small veins. Mirror with one dividing vein. Hind tibiae 0.68-0.86 times as long as hind femora.

KEY TO GENERA OF TURANOGRYLLII

1 Epiphallic lobes with a narrow, finger-like projection; epiphallic lobes strongly serrated: .... *Turanogryllus*

1' Epiphallic lobes without a narrow, finger-like projection 2

2 Virga of male genitalia serrated; epiphallus relatively short and inconspicuous when compared ectoparameres (Figs. 8-10, Otte 1983) .... *Afrogryllopsis*

2' Virga not serrated; epiphallus prominent and conspicuous .... *Neogryllopsis*

TURANOGRYLLUS Tarbinsky

TYPE SPECIES. *Turanogryllus lateralis* (Fieber)

The genus *Turanogryllus* had been described by Tarbinsky (1940) with *Gryllus lateralis* Fieber as the type species. Randell (1964) placed the genus in a new tribe, Gymnogryllini, under the subfamily Gryllinae, on the basis of a study of the male genital apparatus, and Chopard (1967) followed this scheme. Subsequently, other species were included in the genus, three of them from Africa (*niloticus* from Egypt, *scenicus* from Liberia, and *machadoi* from Angola) (Chopard 1967: 34). In this paper I have transferred two additional species from *Gryllopsis* (*flavolateralis* Chopard and *microlyra* Chopard) and I have found four new species in museum collections. Thus the number of African *Turanogryllus* increases from three to nine species.

RECOGNITION OF GENUS. Epiphallic lobes each with terminal finger-like process; ectoparameres with strong serrations and made up of two large lobes. Body color dark brown on dorsum, very pale on sides. Dorsum of head with or without prominent longitudinal stripes, usually dark brown to black; median ocellus on front of face and not visible from above. Head narrower than pronotum. Pronotum narrower anteriorly. Foretibiae with small inner and large outer tympanum. Forewings 2.5-2.9 times as long as pronotum. Chord veins strongly bent.

Turanogryllus niloticus (Saussure)

I did not examine this species. The male genitalia (Fig. 2) which are copied from Randell (1963), are quite distinct from those of the other species treated here.

Turanogryllus scenicus (Gerstaecker)

I did not examine this species. The male genitalia illustrated by Randell (1964, Fig. 4) show that it is distinct from the species treated here.

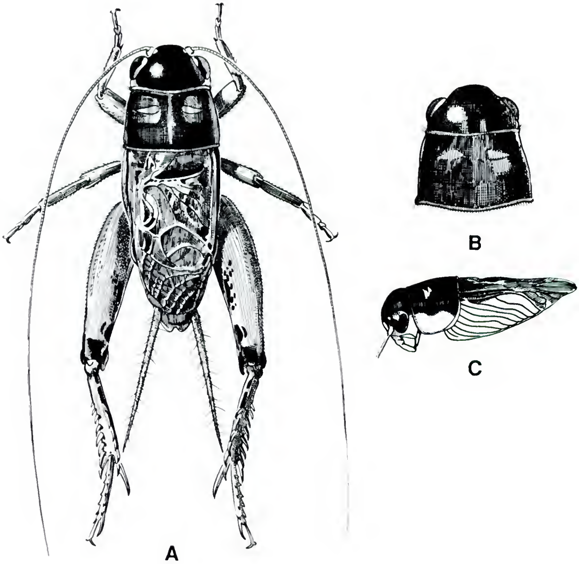


FIG. 5. A, *Turanogryllus kitale* holotype. B, C, *Turanogryllus nimba* holotype.

Turanogryllus flavolateralis (Chopard)

Gryllopsis flavolateralis Chopard 1934: 31. *Holotype M*, Congo [Zaire], Haut Uele Watsa 1922 (L. Burgeon). TERVUREN. Type examined. NEW COMBINATION.

NOTES ON HOLOTYPE. Figs. 6J-7A. Table 2. *Head:* dorsum black, unbanded; three large ocelli; face ivory below median ocellus and below level of antennae; cheeks ivory. *Pronotum:* covered with very fine pubescence, without bristles; dorsum blackish, lateral lobes ivory. *Forewings:* dorsum brown, lateral field with dark band along dorsal margin, pale below that. *Abdomen:* dorsum blackish, venter pale; cerci pale. *Legs:* all pale brown. Foretibiae: basal tarsomere 2.86 times as long as tibiae. *Hindlegs*: lost.

Turanogryllus microlyra (Chopard)

Gryllopsis microlyra Chopard 1938: 55. *Holotype M*, Sierra Leone, Njala, 17 iv 1930 (H.Hargreaves). LONDON. *Turanogryllus*, Randell 1964: 1571. *Gryllopsis*, Chopard 1967: 30. Type examined.

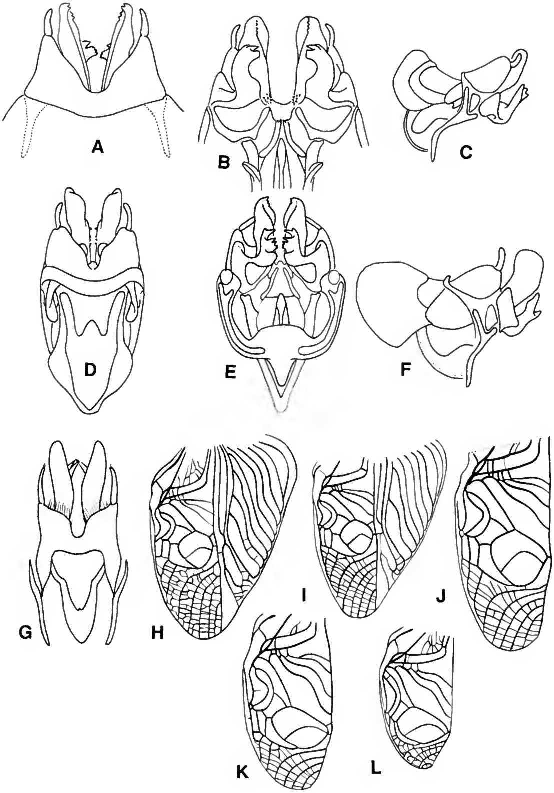


FIG. 6. *Turanogryllus* male genitalia (dorsal, ventral and lateral views). **A-C,** *lateralis* (after Randell 1964, not holotype); **D-F,** *niloticus* (after Randell 1964, not holotype); **G,** *machadoi* holotype (after Chopard 1961, not holotype); **H,** *microlyra*; **I,** *nimba* holotype; **J,** *flavolateralis* holotype; **K,** *sombo*

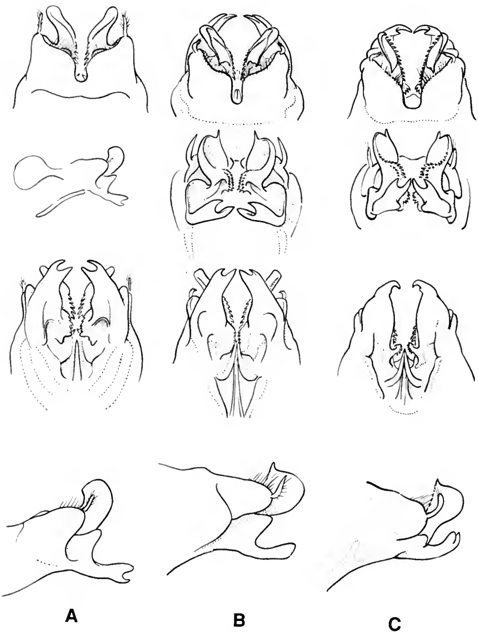


FIG. 7. *Turanogryllus* male genitalia (top to bottom: dorsal, posterior, ventral, and lateral views). A, *flavolateralis* holotype; B, *sombo* holotype; C, *mau* holotype.

NOTES ON HOLOTYPE. Figs. 4H, 8A. Table 2. Dorsum of body, especially head and pronotum dark brown to black, sides and venter ivory colored. Head: dorsum black, shiny, pubescent only on occiput, with a thin median pale stripe; forehead suture T-shaped rather than Y-shaped; all ocellit large; face ivory, but with dark brown bands descending along upper margin of antennal sockets; cheeks pale below level of eyes. Pronotum: dorsum dark brown to black, amrking of muscle attachment plates more pale; lateral lobes balck on upper third, ivory on lower two-thirds. *Forewings:* dorsum medium brown; lateral field pale but dark brown between upper three veins. *Hindwings:* extending two pronotal lengths beyond abdomen. *Fore- and midlegs:* pale brown. *Hindlegs:* femora orange brown with faint darker oblique stripes on outer face; darker around knees, especially on inner face; tibiae pale brown..

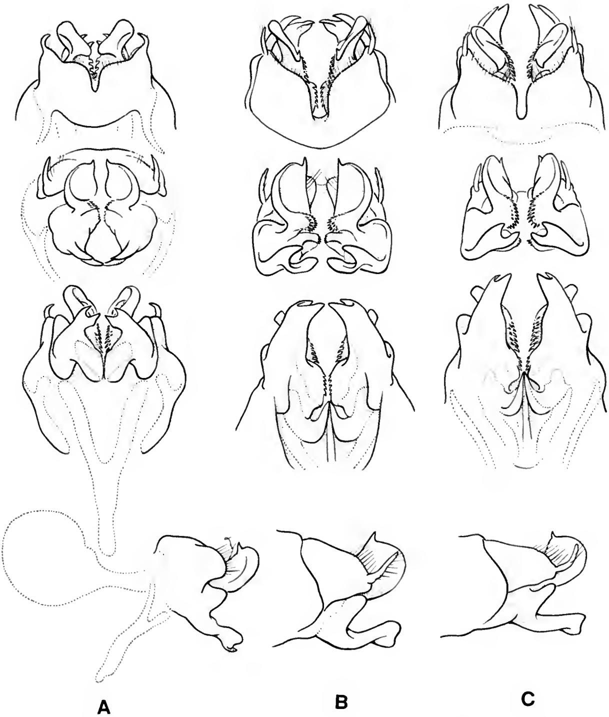


FIG. 8. *Turanogryllus* male genitalia (dorsal, posterior, ventral and lateral views). A, *microlyra* holotype; B, *nimba* holotype; C, *kitale* holotype.

Turanogryllus nimba n. sp.

TYPE. *Holotype M*, Guinea, Nimba, xii 1956-v 1957 (Amjet & Vanderploetsen). PARIS.

RECOGNITION. Figs. 5B,C, 6I, 8B. Table 2. Very similar to *microlyra*, differs in shape of epiphallus and ectoparameres, occiput with four pale stripes.

Males: Head: dark brown, appears black, but with four pale bands on occiput; these do not extend onto vertex; face entirely pale below median ocellus; cheeks pale. *Pronotum:* dorsum very dark brown, nearly black, but muscle attachment plates pale brown; lateral lobes ivory, becoming black at upper margin. *Forewings:*

TABLE 2. Species measurements (for abbreviations see Table 1).

	No. file teeth	BL	FL	CL	FWL/PL	TL/FL	OL/FL	Tymp	sub-apical spurs
Turanogryllus flavolateralis									
HM	205	14	-	-	2.5	-	-	-/O	-
Turanogryllus kitale									
HM	189	15	11	-	2.6	0.77	-	i/O	-
Turanogryllus microlyra									
HM	119	20	12.6	10	2.9	0.8	-	i/O	6/7
Turanogryllus sombo									
HM	121	12	9	-	2.6	0.76	-	i/O	5/6
Turanogryllus mau									
HM	69	14	9.8	8	2.4	0.71	-	i*/0	5/6
Turanogryllus nimba									
HM	135	19	12.5	10	2.4	0.75	-	i/O	6,7/7
PM	163	18	11.5	-	2.3	0.75	-	i/O	6/6
PF	-	17	12	9	2.6	0.76	-	i/O	6/7

dorsum medium brown; lateral field pale, dark brown between upper three veins. *Hindwings:* long, extending two pronotal lengths beyond forewings in holotype; not visible in paratype. *Abdomen:* dorsum dark brown but posterior margin of each tergite pale; venter pale. *Fore- and midlegs:* ivory-colored. *Hindlegs:* femora with oblique rows of brown spots on outer face; tibiae pale brown.

Females: similar to males, hindwings extending two pronotal lengths beyond forewings.

SPECIMENS. *Holotype* M, PARIS. *Paratypes:* 1M, Guinea, Nimba, vi 1942 (Lamotte), PARIS. 1F, same data as holotype, PARIS.

Turanogryllus kitale n. sp.

TYPE. *Holotype M,* Kenya, Kitale Camp Site, 15 iii 1977 (C.C. and A. D. Townsend). LONDON.

RECOGNITION. Figs. 5A, 8C. Table 2. Differs from *sombo* and *mau* by lacking occipital stripes. Most similar to *microlyra* and *nimba*, but differing in the male genitalia.

Males: dorsum dark gray-brown to black on head and pronotum. *Head:* dorsum without stripes; face black above and ivory below median ocellus; cheeks pale to upper level of eyes. *Pronotum:* dorsum black but with 2 large orange patches in anterior half, one on either side of midline; lateral lobes ivory, becoming black at upper margin. *Forewings:* dorsal field gray brown; lateral field pale, dark between upper 3 veins. *Abdomen:* dorsum dark; venter very pale. *Fore- and midlegs:* pale brown to straw colored. *Hindlegs:* femora pale, with oblique rows of brown spots on outer face; and large dark patches on inner face; tibiae pale brown.

SPECIMENS. *Holotype* M, LONDON.

Turanogryllus sombo n. sp.

TYPE. *Holotype M,* N. Rhodesia, [Zambia], N of Lake Bangweulu, N'Sombo, 11 xii 1946. LONDON.

RECOGNITION. Figs. 6C, 7B. Table 2. Most similar to *mau* from which it differs in the male genitalia.

Head: dorsum with four distinct longitudinal stripes; face very pale below median ocellus; cheeks entirely pale to above eyes. *Pronotum:* dorsum darkest along lateral margin and through enctral area, two lighter areas, one on either side of midline; lateral lobes ivory-colored becoming black at dorsal margin. *Forewings:* dorsum gray brown; lateral field pale, dark brown between upper three veins. *Hindwings:* hidden. *Abdomen:* dorsum dark brown; venter very pale. *Legs*: Fore- and midlegs pale; hind femora pale, outer face with oblique rows of pale brown spots; hindtibiae pale.

SPECIMENS. *Holotype* M, LONDON.

Turanogryllus mau n. sp.

TYPE. *Holotype M*, Kenya, Mau Mau, 9 iii 1982 (C. F. Dewhurst). LONDON.

RECOGNITION. Figs. 6L, 7C. Table 2. Distinguished from *mau* by the male genitalia.

Black and gray on dorsum; pale gray to white on sides and venter. *Head:* dorsum with four longitudinal stripes on vertex and occiput; pale behind eyes; face very pale below median ocellus; cheeks entirely pale to above level of eyes. *Pronotum:* dorsum largely black but pale brown on muscle attachment plates and just anterior to muscle attachment plates; lateral lobes ivory, becoming black at upper margin. *Forewings:* dorsum gray brown; lateral field pale, brown between top two veins. *Hindwings:* hidden. *Abdomen:* dorsum dark brown; venter very pale. *Legs:* Fore- and midlegs; femora pale with small dark spots on upper face; tibiae pale with golden to coppery pubescence. *Hindlegs*: outer face with faint oblique rows of gray spots; tibiae pale.

SPECIMENS. *Holotype* M, LONDON.

AFROGRYLLOPSIS Randell

This genus was revised by Otte 1983. The status of this name remains conditional upon an examination of males of *Podogryllus* Karsch. Presently that genus is known only from females. Should the males of *Podogryllus* prove to be congeneric with *Afrogryllopsis*, then the latter name will be synonymized.

Afrogryllopsis aruensis Otte 1983: 233.

NEW RECORD. A male from Garamba, Congo, 14 v 1912 (Land & Chapin). PHILADELPHIA. Genitalia virtually indistinguishable from the holotype and with approximately 1170 file teeth (holotype with approximately 1000 teeth).

Afrogryllopsis charliersi (Chopard)

Podogryllus charliersi Chopard 1934: 83. *Holotype* F, Congo, Kinda, 2 ix 1914 (L. Charliers). TERVUREN. Type examined. NEW COMBINATION.

NOTES ON TYPE. Body color mottled brown. Head with dark brown on top, with broad pale band across vertex and pale band connecting lateral ocelli. Face entirly pale below median ocellus. Pronotum with numerous small, somewhat indistinct brown spots on dorsum, pale on lateral lobes. Dorsum of abdomen with numerous small dark brown spots, these becoming larger posteriorly on abdomen and coalescing to form larger markings arranged in transverse rows. Forewings about half as long as pronotum, triangular in dorsal view, separated by a wide gap. Foretibiae with a small inner and a large outer tympanum. Legs all pale brown, but hind femora with faint oblique brown streaks on outer face and with black crescents on knees. Body length ca. 26 mm; hind femur length 19.5 mm; ovipositore bent, longer than hind femora, but shorter than body.

PODOGRYLLUS Karsch

Podogryllus desultorius Karsch

Podogryllus desultorius Karsch 1893: 150.

I have examined the female type of this species; it resembles the females of *Afrogryllopsis* closely. Since no males of this genus have ever been described it remains a possibility that all *Afrogryllopsis* species will belong to the genus *Podogryllus*.

GRYLLINAE: GRYLLINI

DAMARACHETA n. gen.

TYPE SPECIES. *Damaracheta schultzei* (Karny)

The species belonging to the genus *Damaracheta* have accumulated over a period of several years. The first member of the genus was a male from Damaraland found in the Philadelphia collection; this male later proved to be the first male of Karny's *Acheta schultzei* (a species later transferred to *Modicogryllus* by Chopard, 1961). A male and a female from the South African Museum in Capetown proved to be a second species, *capensis*. Finally, in a recent collecting trip to Malawi, I collected three additional species. The genus appears to be closely related to *Gryllus*, but possesses genitalic features which suggest a closer relationship to *Platygryllus*. The Malawi species are found in habitats typical for field crickets, but nothing is known about the biology of Botswana and South African species.

RECOGNITION OF GENUS. Differs from all other genera in having elongate epiphallus, elongate ectoparameres, and very long convoluted spermatophore tube mold.

Body color variable, dark brown to pale brown on dorsum; pronotum with characteristic color pattern (Fig. 9). Body length 20-23 mm. Forwing 2.7-3.5 times as long as pronotum. Hindtibiae 0.7-0.8 times as long as hindfemora. Ovipositor 1.6 to 2.0 times as long as hindfemora. Inner tympanum small and round, outer one much larger and oval. Hindtibiae with 5 or 6 inner and 6 outer subapical spurs.

RELATIONSHIP. The trilobed epiphallus of *D. capensis* shows clearly that the genus is closely related to the genus *Gryllus*.

Damaracheta schultzei (Karny)

Acheta schultzei Karny 1910: 43. *Holotype F*, Bechuanaland, Botswana, Leclake-Lekututu, Jan 1905 (L. Schultze S.). BERLIN. *Modicogryllus*, Chopard 1961: 275. Type examined. NEW COMBINATION.

RECOGNITION. Figs. 9AB, 11A-C. Table 3. Differs from *capensis* as follows: epiphallus bilobed; abdominal tergum pale brown centrally; vertex strongly striped; forehead with pale stripe connecting lateral ocelli.

Male: Medium in size; ivory-colored with strongly defined dark brown markings on pronotum and head. Head: dorsum dark brown with ivory bands; with three ocelli; face ivory below median ocellus; cheeks ivory. Pronotum: dorsum with large patches of dark brown; lateral lobes with a scattering of small brown spots along upper margin, otherwise very pale. Forewings: dorsum and lateral field straw-colored. Hindwings: extending about one pronotal length beyond forewings. Abdomen: dorsum variegated with ivory and dark brown markings; distal tergites largely pale, proximal tergites dark brown; all tergites brown on sides with pale spots; venter pale brown. Male genitalia: Epiphallus slender, bilobed, with pronounced U-shaped cleft; ectoparameres very long and slender; spermatophore tube mold exceedingly long and convoluted—probably exceeding the body length; virga very long and slender. Front and middle legs very pale brown; inner tympanum small and round, outer one large, oval. Hindlegs: femur pale brown but with distinct oblique stripes on outer face; tibiae with 6 inner and 6 outer subapical spurs.

Female (HOLOTYPE). Very similar to male (see Table 3).

HABITAT. Not certain. A male was taken at Damara Pan in Botswana.

SPECIMENS. *Holotype* F, BERLIN. Botswana, Damara Pan, 15-21 iv 1930 (v. -L Kal. Exped.) 1M, PHILADELPHIA.

Damaracheta capensis n. sp.

TYPE. *Holotype M* , South Africa, Cape Province, Beaufort West District, S. A. M. 2. 58. PRETORIA.

RECOGNITION. Figs. 10C, 11D-G. Table 3. Differs from *schultzei* as follows: epiphallus

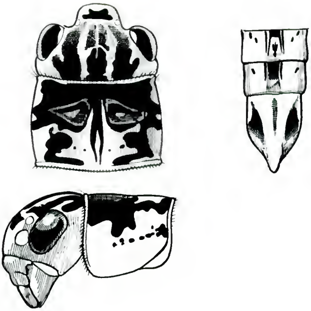


FIG. 9. A, B, *Damaracheta schultzei* head and pronotum. C, *Damaracheta kasungu* venter of last three abdominal segments.

trilobed; abdominal tergum largely dark brown; forehead without pale stripe connecting lateral ocelli.

Male: Very similar to male of *schultzei*, especially in the pronotal pattern, but body generally darker, especially on dorsum of head where only two somewhat indistinct pale stripes visible and on dorsum of abdomen which is dark throughout its length. *Fore- and midlegs:* pale brown, with two rows of brown markings along outer and inner faces near forsal side. *Hindwings:* extending well beyond end of abdomen.

Female: Colored like male, but dorsum of head without any longitudinal pale stripes. Ovipositor very long (Table 3).

SONG. Not known.

SPECIMENS. *Holotype* M, PRETORIA. *Paratype:* Same data as holotype, 1F, PRETORIA.

Damaracheta mlozi n. sp.

TYPE. *Holotype M,* Malawi, Lake Malawi National Park, nr. Monkey Bay, 23 iii 1986 (Otte, Glenn, & Ruffin). PHILADELPHIA.

RECOGNITION. Figs. 10D, 12A-C, 13. Tables 3, 4. Differs *schultzei* and *capensis* in body color and shape of male genitalia.

Body color dark brown to black, head almost entirely black. *Head:* dorsum black, without occipital stripes; with a pale ring around the eyes; face black but lower half of clypeus pale; cheeks blackish but bases of mandibles pale. *Pronotum:* dorsum entirely black in anterior half, with small (holotype) or larger (paratype) pale areas in posterior lateral corners; lateral lobes mostly black but pale along lower anterior margin. *Forewings:* dorsum darkish, but somewhat pearly-opaque in chordal and apical areas; lateral field mostly transparent, but dark brown to black along upper margin. *Hindwings:* hidden, as long as pronotum. *Abdomen:* dorsum black with rows of pale markings (4 pale markings on each tergite. *Front and middle legs:* largely black but with pale on lower face. *Hindlegs:* Femora largely dark brown, but lower anterior part of outer face pale brown; outer face with dark oblique stripes (most conspicuous against the pale areas); upper face with pale patch just before knees. Tibiae black.

SONG. Fig. 13.

HABITAT. Miombo woodland and acacia woodland, in deep grass.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratype:* Same data as holotype, 1M, PHILADELPHIA.

Damaracheta kasungu n. sp.

TYPE. *Holotype M,* Malawi, Kasungu National Park, Lifupa Lodge, miombo woodland, 33 08E 13 06S, 18 iii 1986 (Otte & Glenn 155). PHILADELPHIA.

RECOGNITION. Figs. 9D, 10A, 12D-F, 13. Tables 3, 4. Differs from *zomba* in having a white patch on pronotal lateral lobes hind femora which are not entirely black and in length of spermatophore tube mold and number of file teeth.

Male: Body color black, becoming pale on venter. *Head*: dorsum black, but eyes with narrow ivory ring; face black, becoming variegated

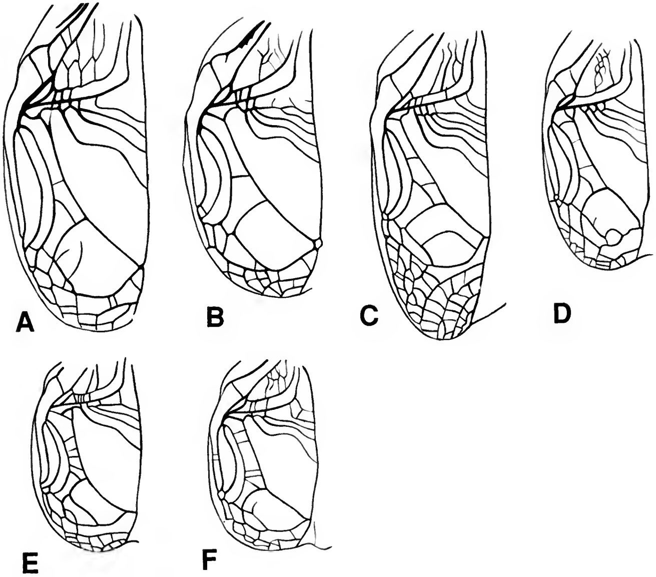


FIG. 10. Forewings of holotypes of *Damaracheta* and *Gryllus*. A, *D. kasungu*; B, *D. zomba*; C, *D. capensis*; D, *D. mlozi*; E, *Gryllus kapushi*; F, *G. mzimba*.

dark brown and ivory on clypeus and labrum; cheeks black; maxillary palpi mostly black but penultimate segment white on upper face. *Pronotum*: dorsum black; lateral lobes largely black but with an ivory oval patch in lower anterior corner. *Forewings*: dorsal field largely black but with pale veins in basal, mirror, and apical areas, and with narrow pale line along inner side of M vein; lateral field black but most Sc branches pale. File teeth with long wings. *Hindwings*: hidden, about as long as pronotum. *Abdomen*: dorsum black; venter pale, but marked with black spots and patches as shown in figure. *Fore- and midlegs*: femora black but ivory along venter; tibiae black. *Hindlegs*: femur black on upper face, turning gradually paler with pale oblique stripes on outer face; lightest in lower anterior quarter; tibiae black.

SONG. Consists of one two three separate pulses followed immediately by a short trill. Only a very poor tape recording of this species was made and the possibility remains that it was a courtship song.

HABITAT. The only male collected was in a wet patch of grass a few meters from a small lake (artifial dam) in miombo woodland.

SPECIMENS. *Holotype* M, PHILADELPHIA.

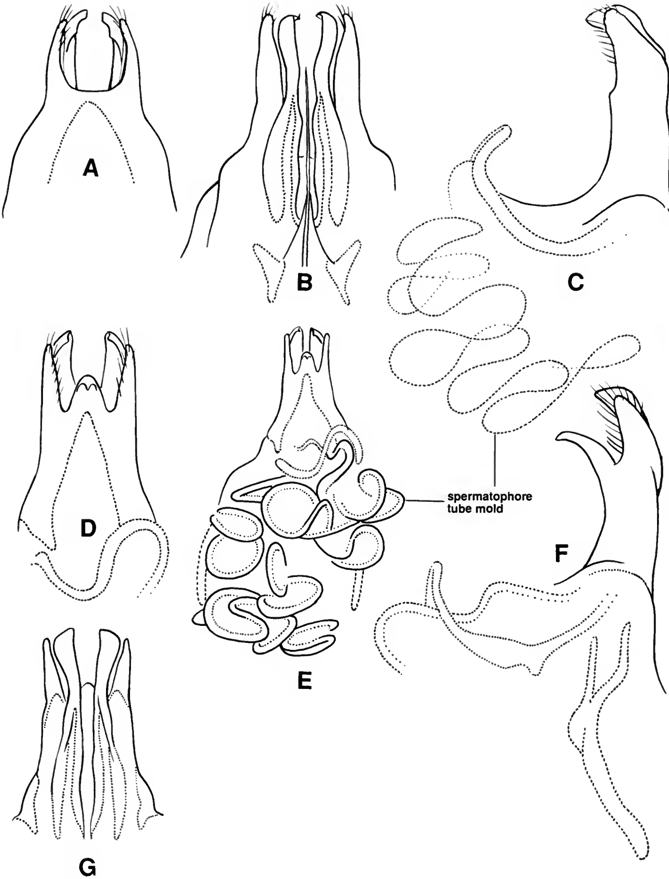


FIG. 11. *Damaracheta* male genitalia. **A-C**, *schultzei* (not holotype); **D-G**, *capensis* holotype.

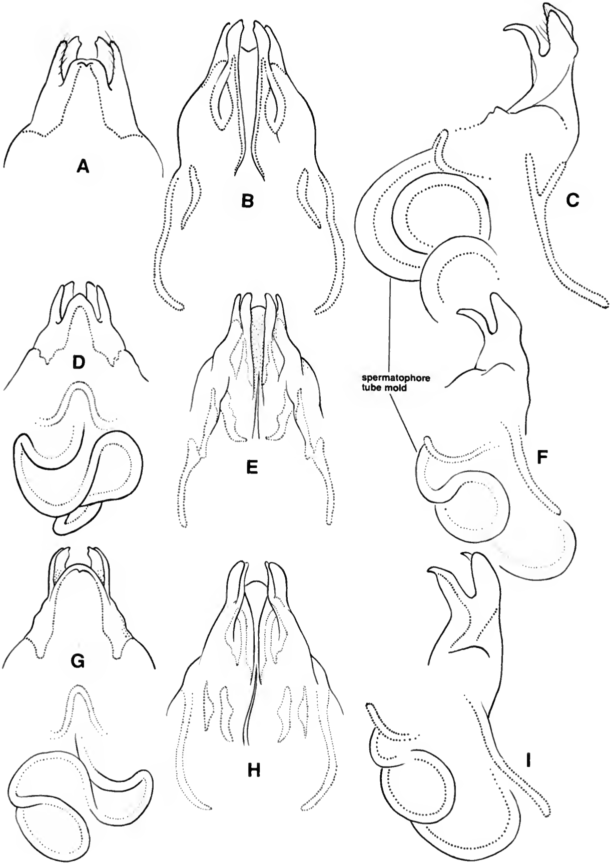


FIG. 12. *Damaracheta* male genitalia (dorsal, ventral and lateral views). **A-C**, *mlozi* holotype; **D-E**, *kasungu* holotype; **G-I**, *zomba* holotype.

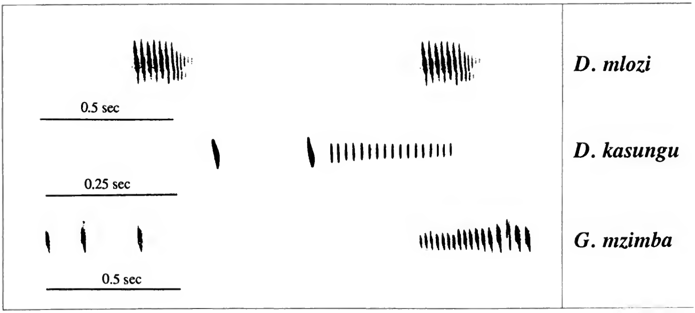


FIG. 13. *Damaracheta* and *Gryllus* songs. The song of *kasungu* may have been part of courtship.

Damaracheta zomba n. sp.

TYPE. *Holotype M*, Malawi, Zomba Plateau, above Zomba, ca. 1400 m, 4 iv 1986, 35 19E 15 22S (Otte, Glenn, & Ruffin). PHILADELPHIA.

RECOGNITION. Figs. 10B, 12G-I. Table 3. Differs from *kasungu* as follows: file with fewer than 90 teeth; lateral lobes without pale patch; lateral epiphiphallic lobes wides, spoon-shaped in lateral profile. Body color nearly black (holotype is entirely black, paratype shows indistinct reddish patterns on head and pronotum).

Head: dark brown with faint brownish stripes on occiput or entirely black; face and cheeks largely black. *Pronotum*: dorsum black or slightly variegated black and dark reddish brown; lateral lobes black. *Forewings*: dorsal field black in holotype, mostly black in paratype but with lighter veins in apical area; lateral field black. *Abdomen*: dorsum black; venter light brown but each sterninte with two narrow longitudinal stripes, two small dark spots and dark lateral margins. *Fore- and midlegs:* black. *Hindfemora*: black in holotype, and with oblique black and reddish stripes on outer face in paratype.

SONG. The song was not tape recorded. In my notes I indicated that it consisted of "long chirps."

HABITAT. We discovered this species on a grassy slope on top of the Zomba plateau. Males were singing in the afternoon but did not sing after dark.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratype:* 1M, same data as holotype, PHILADELPHIA.

GRYLLINI

GRYLLUS Linné

The African members of this genus were recently revised by Otte and Cade 1984c.

Gryllus kapushi n. sp.

TYPE. *Holotype M*, N. Rhodesia [Zambia], Kapushi, 2 i 1928 (M. Burr). LONDON.

RECOGNITION. Figs. 10E, 14A. Table 3. Most similar to *carvalhoi* from Angola, but differs in shape of male epiphallus (see Otte & Cade 1984c, Fig. 8B). Like *carvalhoi* the forehead is extremely wide, and head turns from pubescent and

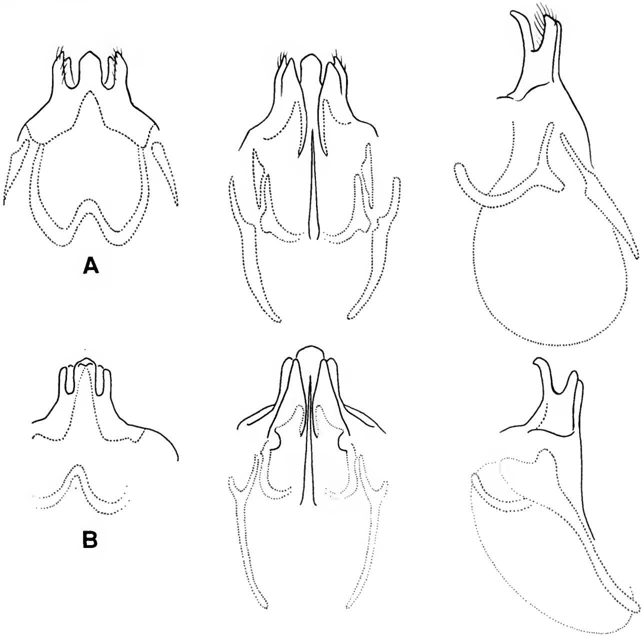


FIG. 14. *Gryllus* male genitalia (dorsal, ventral and lateral views). A, *kapushi* holotype; B, *mzimba* holotype.

pale brown on vertex to glabrous and black on forhead.

Males: Body color reddish brown, but face, forehead and lateral lobes black. *Head*: pubescent and pale brown on occiput and vertex, turning to glabrous and black between eyes; median ocellus located well forward on the head so that it is invisible from above; forehead without pale stripes between lateral ocelli; face dark brown to black, shiny; mouthparts reddish; cheeks blackish, transition to brown occurs at upper side of eyes. *Pronotum*: dorsum more or less uniformly reddish brown; lateral lobes blackish. *Forewings:* reddish, mirror small. *Hindwings:* small, narrow, about half as long as pronotal length. *Abdomen*: dorsum blackish, venter pale brown, but subgenital plate dark brown. *Legs* deep reddish brown, somewhat mottled with dark brown and small pale spots; hindfemora with dark reddish brown oblique stripes on the outer face, dark reddish brown with small pale spots on dorsal face.

Female: Similar to male in size and color, but dorsum of abdomen reddish brown, mottled with

TABLE 3. Species measurements (for abbreviations see Table 1).

	No. file teeth	BL	FL	CL	FWL/PL	TL/FL	OL/FL	Tymp	sub-apical spurs
Damaracheta schultzei									
HF	-	20	12	-	1.9	-	1.6	i/O	5/6
M	183	21	13.5	-	2.7	0.71	-	i/O	6/6
Damaracheta capensis									
HM	153	22	11.5	-	3.3	0.78	-	i/O	6/6
PF	-	21	13	-	3.5	-	2	i/O	6/6
Damaracheta mlozi									
HM	116	21	14	-	2.3	0.78	-	i/O	6/6
PM	-	21	15	16	2.1	-	-	i/O	-
Damaracheta kasungu									
HM	115	18	12.5	-	2.63	0.8	-	i/O	6/6
Damaracheta zomba									
HM	83	17	10.8	10.0+	2.35	0.76	-	i/O	6/6
PM	79	18	11.5	10.0+	2.43	0.78	-	i/O	5/6
Gryllus kapushi									
HM	122	17	12.2	-	2.3	0.78	-	-/O	6/7
PM	-	18	12	-	2.2	0.79	-	-/O	6/7
PF		17	12	-	0.9	0.83	0.67	i/O	6/6
Gryllus mzimba									
HM	102	10.5	11.0+	-	2.6	0.81	-	-/O	4/5,6

small dark spots, and lateral pronotal lobes not black, though darker than dorsum. Forewings triangular (dorsal view), barely overlapping at midline. Hindwings absent. Ovipositor shorter than hind femora.

SPECIMENS. *Holotype* M, LONDON. *Paratypes:* Same data as holotype, 1F, LONDON; 1M, PHILADELPHIA.

Gryllus mzimba n. sp.

TYPE. *Holotype M,* Malawi, 12 km south of Mzimba, 21 iii 1986 (Otte and Glenn). PHILADELPHIA.

RECOGNITION. Figs. 10F, 13, 14B. Tables 3, 4. Body color blackish, but with pearly white coloration in chordal and apical regions of forewings; occiput with six pale stripes, lateral most one much ligher and wider than more medial ones; hind femora with distinct dark oblique stripes on outer face. Dorsum of abdomen with small white spots.

Size medium, color reddish to black, with pearly white on forewings and with striped hind femora. *Head*: dorsum black, with six pale occipital stripes, lateral most ones widest and palest. Median ocellus on front of face and not visible from above. Face black down to middle of clypeus; cheeks black with small pale spot next to lower posterior margin of eye. *Pronotum:* dorsum dark reddish borwn, black in center and along posterior margin, lighter in posterior lateral quarter; lateral lobes black but with small pale spot near anterior end. *Forewings:* dorsal field dark, but milky with pale veins in chordal and apical areas and on median fan; lateral field black. *Hindwings:* very short, ca. one third the length of the pronotum. *Abdomen* : Dorsum black; three tergites anterior to last tergite with

TABLE 4. Song parameters of *Damaracheta* and *Gryllus*. p/s, pulses per second; ch/s, chirps per second; p/ch, pulses per chirp; KHz, midpoint of frequency in kiloHerz; •C, temperature. Localities: 155, Kasungu National Park, Lifupa Lodge. 160, Viphya Highlands, 12 km south of Mzimba. 162, Lake Malawi, Cape Maclear.

	p/s	ch/s	chirp length (or p/ch)	KHz	°C
Damaracheta mlozi					
Loc 162	48.9-69.8	0.69	0.21	5.2	84
Loc 162	46.6-77.3	1.02	0.20	4.6	84
Damaracheta kasungu					
Loc 155	[12.3 (tick rate)	64.2 (trill rate)	0.25 (trill length)]	3.6	66
Gryllus mzimba					
Loc 160	6.2 (ticks) 31.0-50.8	0.38-0.42	3.7	64	
Gryllus krugeri					
Loc 162	69.9	1.14	(5-6)	4.5	74
Loc 162	88.0	1.23	(5)	4.4	78

two lateral pale spots; venter ivory colored, subgenital plate dark brown. *Fore- and midlegs:* femora mostly dark brown but with small pale spots on upper and outer faces; tibiae dark brown and plack with small pale spots on upper face. *Hindlegs:* femur: dorsum dark reddish brown but with large paler patch just before knees; outer face pale in lower anterior part and with distinct dark oblique stripes; tibiae dark brown.

SONG. The song consists of one to three separate pulses (delivered at variable rates) followed by a chirp of about one second duration.

HABITAT. Found singing in grassy understory in miombo woodland on the Viphya Plateau..

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratype:* 1F, Malawi, 13 km east of Mzimba, 21 iii 1986 (Otte & Glenn). PHILADELPHIA.

Gryllus subpubescens (Chopard)

Liogryllus subpubescens Chopard 1934: 20. Holotype F, Congo, Elizabethville, 27 iv 1927 (Dr. Stappers). TERVUREN. Type examined. *Gryllus*, Chopard 1961: 270.

This species does appear to be a *Gryllus* on the basis of coloration and the pubescence, however, until a male of the species can be examined the possibility remains that it belongs to *Damaracheta.*

MODICOGRYLLINI

VELARIFICTORUS Randell

Velarifictorus changus n. sp.

TYPE. *Holotype M*, N. Rhodesia [Zambia] N'Changa (C. T. Macnamara). LONDON.

RECOGNITION. Figs. 17F, 18C. Table 5. Differs from other *Velarifictorus* in male genitalia and in having black forehead with white band.

Head: reddish on vertex and occiput; becoming black on forehead, with broad white interocellar white band, and with narrow pale median line descending from median ocellus to epistomal suture; mouthparts reddish; face black; cheeks posterior to and below eyes dark brown to black. *Pronotum:* dorsum unicolorous red-brown; lateral lobes blackish, extreme lower margin pale; lower edge black. *Forewings:* dorsum medium to dark brown; lateral field dark brown to black. *Hindwings:* micropterous. *Abdomen:* dorsum dark brown; venter medium brown. *Fore- and midlegs:* femora brown with prominent dark marks on upper face, and large dark marks on inner and outer faces at distal end. *Hindlegs:* femora reddish with oblique stripes of darker color on outer faces; tibiae reddish, black at bases of each spur.

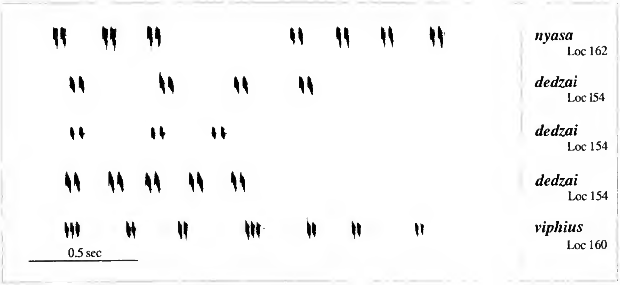


FIG. 15. *Veralifictorus* songs. Although the songs of *nyasa* and *dedzai* are very similar, the species are very different. Three *dedzai* songs are given to show variation in the chirp rate.

Velarifictorus ghanzicus n. sp.

TYPE. *Holotype M,* Botswana, 40 miles SW of Ghanzi 29 x-9 xi 1961 (Haacke & Prozeski). PRETORIA.

RECOGNITION. Figs. 17C, 19C. Table 5. Very similar to *botswanus,* but differing in the male genitalia (see Otte, Toms and Cade Fig. 29).

Males: Body very pale, sandy or straw-colored. *Head*: distinctly wider than pronotum; dorsum with with 6 longitudinal gray stripes, the middle two separated by very narrow pale stripe; these gray stripes turn dark brown just before forehead suture; forehead with broad pale band running between lateral ocelli, and with dark brown band above middle ocellus; face pale, but with dark brown along lower, inner margins of antennal sockets; cheeks pale. *Pronotum*: dorsum pale with some darker indistinct blotches; lateral lobes with irregular shaped dark stripe along dorsal side, otherwise very pale. *Forewings*: entirely pale. *Hindwings*: tiny, less than one third length of pronotum. *Abdomen:* dorsum pale brown with small dark spots; venter pale. *Fore- and midlegs*: entirely pale. *Hindlegs*: pale.

Females: Not known.

SPECIMENS. *Holotype* M, PRETORIA. *Paratypes:* Same data as holotype, 1M, PRETORIA; 1M, PHILADELPHIA.

Velarifictorus dedzai n. sp.

TYPE. *Holotype M,* Malawi, Dedza, 17 iii 1986 (Otte & Glenn). PHILADELPHIA.

RECOGNITION. Figs. 15, 17D, 18D. Tables 5, 6. Differs from all other other members of this genus in song and the shape of the male epiphallus. Dorsum of body, especially head and pronotum dark brown to black, lower sides and venter ivory colored.

Head: dorsum dark brown to black and with single pale stripe behind margin of each eye; face black with narrow pale stripe descending from median ocellus; clypeus variegated pale and dark brown; cheeks black. *Pronotum:* dorsum very dark brown and with scarcely visible pale markings; lateral lobes black in upper half, ivory in lower half. *Forewings:* dorsum dark brown; lateral field dark brown in upper half. *Hindwings:* hidden beneath forewings, nearly as long as pronotum. *Abdomen:* dorsum dark brown with scattered pale areas; venter ivory colored. *Fore- and midlegs:* femora pale with small black spots. *Hindlegs:* femora pale with oblique stripes on outer face, knees dark brown; tibiae pale brown above, dark brown underneath.

SONG. Fig. 1. Short bursts of double-pulse chirps.

HABITAT. Miombo woodland. Males were

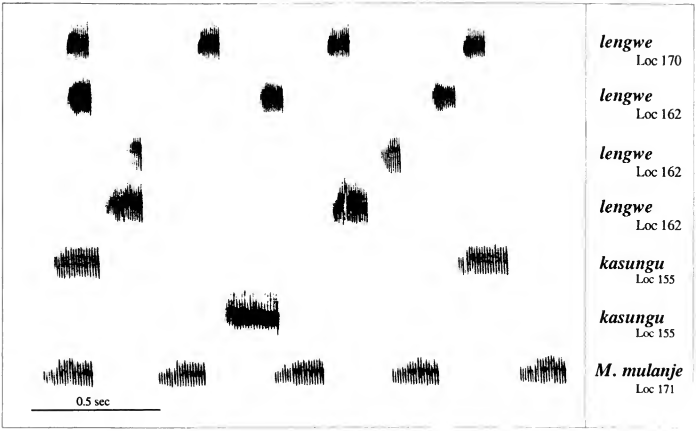


FIG. 16. *Velarifictorus* songs. Several *lengwe* and *kasungu* songs are given to show variation in chirp length and chirp rate.

found singing in crevices among large exposed rock faces.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratype:* Same data as holotype, 1M, PHILADELPHIA.

Velarifictorus kasungu n. sp.

TYPE. *Holotype M,* Malawi, Kasungu National Park, 18 iii 1986 (Otte & Glenn). PHILADELPHIA.

RECOGNITION. Figs. 16, 17EH, 19A. Tables 5, 6. Very similar in genitalia to *V. natus* (Otte, Toms, & Cade, in press), but median lobe of epiphallus not as long and median process (surrounding virga) with two narrow lobes, the smaller one attached to base of larger one. Differs from *natus* also in song.

Body color black and ivory. *Head:* dorsum black but with 6 distinct pale longitudinal stripes on occiput and vertex; face pale, epistomal suture stronly arched up toward the median ocellus; cheeks pale. *Pronotum:* dorsum variegated black and ivory; lateral lobes black in upper half, ivory colored in lower half. *Forewings:* dorsal field black; lateral field black in upper half. *Abdomen:* dorsum dark brown and with two rows of pale markings; venter ivory colored but subgenital plate black along lateral margins. *Fore- and midlegs:* femora pale but with small dark spots on upper face and large dark streaks on inner and outer faces expecially at distal end. *Hindlegs:* femora pale with a row of brown marks on the upper face, a series of oblique stripes on the other face and a large irregular dark marking on the inner face.

SONG. A sequence of short chirps with a high pulse rate.

HABITAT. Rock crevices, soil cracks and in shallow burrows in miombo woodland.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratype:* Same data as holotype, 1M, PHILA.

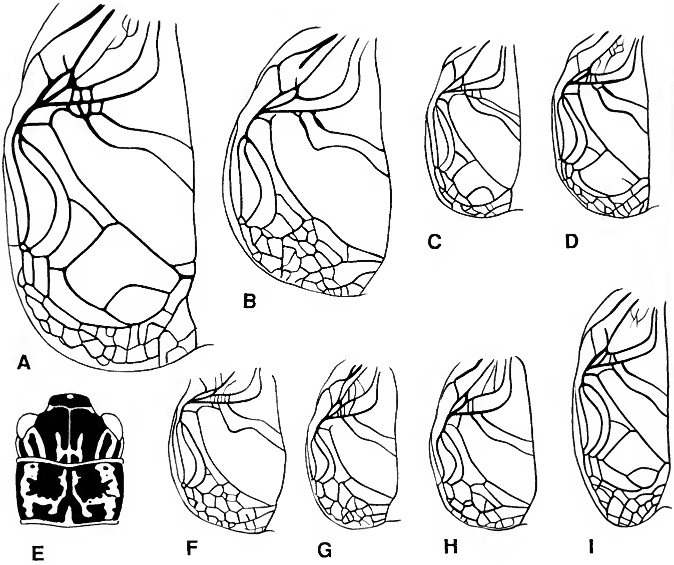


FIG. 17. **A-H,** *Velarifictorus* male forewings and head-plus-pronotum. **A,** *nyasa* holotype; **B,** *viphius* holotype; **C,** *ghanzicus* holotype; **D,** *dedzai* holotype; **E,** *kasungu* head and pronotum; **F,** *changus* holotype; **G,** *lengwe* holotype; **H,** *kasungu* holotype; **I,** *Modicogryllus mulanje* holotype male forewing.

Velarifictorus nyasa n. sp.

TYPE. Holotype M, Malawi, Lake Malawi, Cape Maclear, 34 51E 14 02S, 24 iii 1986 (Otte, Glenn, & Ruffin). PHILADELPHIA.

RECOGNITION. Figs. 15, 17A, 18A. Tables5, 6. Very large for genus, body length more than 25mm; genitalia and song as figured.

Body color dark reddish brown (nearly black) on dorsum, ivory on venter. *Head:* wider than pronotum; dorsum dark reddish brown, with only a small pale streak at upper posterior margin of eyes; frons without a pale line connecting the lateral ocelli; face dark brown to black, somewhate variegated on clypeus and labrum; cheeks dark brown to black but with a yellow streak next to posterior margin of eye; maxillary palpi white. *Pronotum:* wider at anterior end; dorsum variegated dark reddish brown and black but with a pale patch at lateral margins of posterior quarters; lateral lobes black above and ivory below. *Forewings:* dorsal field dark brown to black; lateral field dark brown to black in upper two-thirds, pale below, and with pale Sc branches. *Hind-*

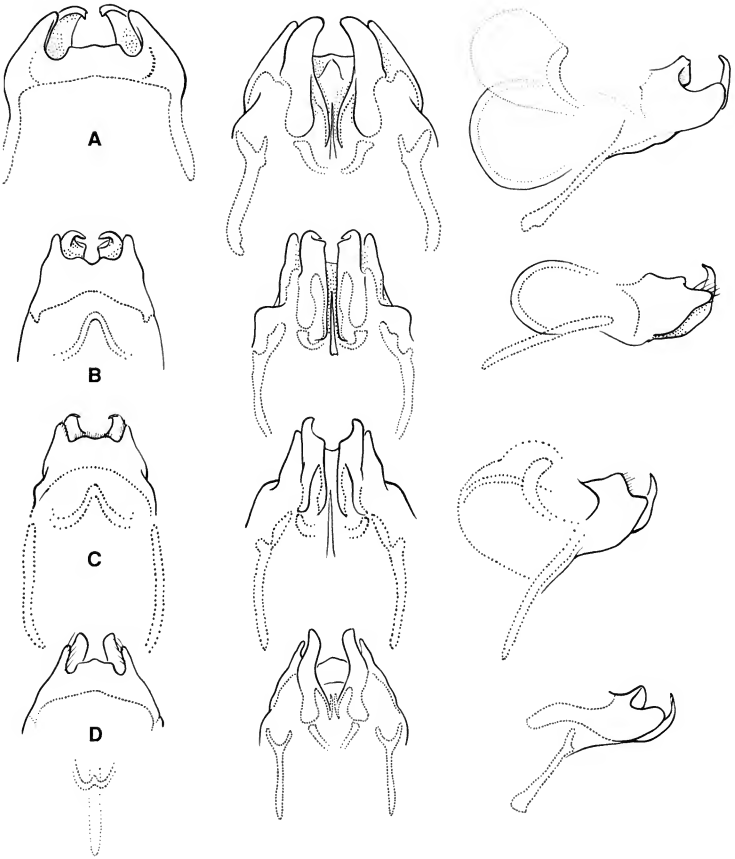


FIG. 18. *Velarifictorus* male genitalia. **A**, *nyasa* holotype; **B**, *viphius* holotype; **C**, *changus* holotype; **D**, *dedzai* holotype.

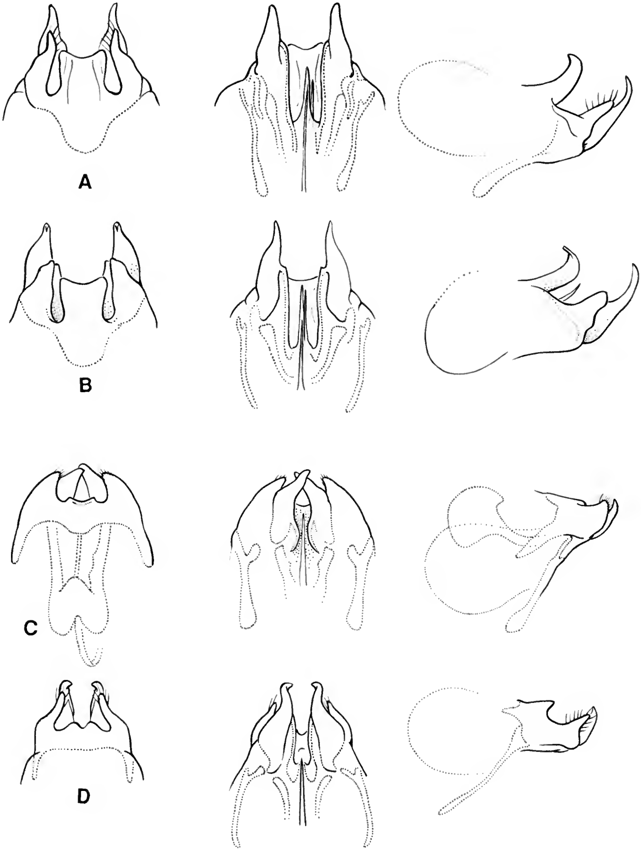


FIG. 19. *Velarifictorus* and *Modicogryllus* male genitalia. **A**, *V. kasungu* holotype; **B**, *V. lengwe* holotype; **C**, *V. ghanzicus* holotype; **D**, *Modicogryllus mulanje* holotype.

TABLE 5. Species measurements (for abbreviations see Table 1).

Species	No. file teeth	BL	FL	CL	FWL/PL	TL/FL	OL/FL	Tymp	sub-apical spurs
Velarifictorus changus									
HM	74	18	10.3	-	2	0.72	-	lost	3/4
Velarifictorus ghanzicus									
HM	76	14	11	13.5	2.6	0.63	-	i/O	5/5
PM	-	13	9.6	12	2.8	0.65	-	i/O	5/5
PM	-	15	10.5	-	2.7	-	-	i/O	5/5
Velarifictorus dedzai									
HM	113	17	10.5	-	-	0.7	-	-/O	5/6
PM	126	18	11.5	14.0+	-	-	-	-/O	-
Velarifictours kasungu									
HM	79	15	8.5	8.8	2.1	0.72	-	-/O	5/6
Velarifictorus nyasa									
HM	137	28	16	22	2.1	0.72	-	-/O	5/5,6
Velarifictorus viphius									
HM	62	ca. 17	10.2		2.4	0.71	-	-/O	5/6
Velarifictorus lengwe									
HM	75	14.5	8	9	1.93	0.71	-	-/O	5,6/7
PM	73	13.2	7.9	7.8	2.04	-	-	-/O	5/6
PM	68	13.5	7.5		1.97	-	-	-/O	5/7
Modicogryllus mulanje									
HM	98	12.5	8	7.5	3.4	0.76	-	i/O	4/5

wings: hidden, about two-thirds as long as pronotum. *Abdomen:* dorsum generally dark brown but darkness is made up of numerous small brown spots; venter pale. *Fore- and midlegs:* pale with many very small dark spots, and one or several larger dark markings on inner faces; tibiae pale but with dark stripe on lower face. *Hind legs:* femora pale with some brownish spots on upper face, large paired dark marks on inner face near distal end, and patch of lighter brown markings anterior to that, and outer face with indictinctreddish brown oblique stripes.

SONG. A sequence of double-pulse chirps.

HABITAT. The holotype was found in a rock crevice in some rocky hills covered in Brachystegia woodland at the southern end of Lake Malawi.

SPECIMENS. *Holotype* M, PHILADELPHIA

Velarifictorus lengwe n. sp.

TYPE. *Holotype M*, Malawi, Lengwe National Park, 28 iii 1986 (Otte, Glenn, & Ruffin 170). PHILADELPHIA.

RECOGNITION. Figs. 16, 17G, 19B. Tables 5, 6. Very similar to *natus* from Botswana (Otte, Toms, & Cade 1987) but lateral lobes of epiphallus wider in lateral aspect, and lateral branck of pseudovirga originating near base and not near middle.Body color dark brown to ivory.

Head: dorsum of head with 8 dark longitudinal bands includind broad bands behind eyes; lateral ocelli connected by a narrow pale line; face and cheeks pale. *Pronotum:* dorsum variegated with dark brown and ivory; lateral lobes black in upper half, ivory in lower half. *Forewings:* dorsal field dark brown, darkest in apical area; lateral field blackish in upper half, transparent in lower half. *Hindwings:* hidden, about two

TABLE 6. Song parameters (for abbreviations see Table 8).

locality	p/s	ch/s	(ch/group)	chirp L (or p/ch)	KHz	°C
Velarifictorus dedzai						
Loc 154	25.1	3.1-3.6	(2-3)	(2)	3.5	16
Loc 154	21.7	3.3	(4)	(2)	3.5	16
Loc 154	25.4	2.6-5.3	(4)	(2)	3.7	16
Velarifictorus nyasa						
Loc 167	23.3	2.3	-	(2)	4.2	18
Loc 162	26.7	4.7	(3-5)	(2)	4.4	24.4
Velarifictorus viphius						
Loc 160	40.2	4.1	-	(2-3)	2.5	18
Velarifictorus kasungu						
Loc 155	88	0.3-0.5	0.23-0.24	-	4.7	19
Loc 155	83	0.56	0.17	-	4.5	19
Loc 155	90.7	0.63	0.21	-	4.6	19
Loc 155	92.4	0.62	0.21	-	4.7	19
Loc 160	72	0.29-0.33	0.24	-	3.7	18
Loc 153	90.3		0.17	-	4.7	21
Loc 153	88		0.2	-	4.3	21
Loc 153	83.4	0.63	0.23	-	4.4	21
Loc 153	91.4	0.56	0.23	-	4.3	21
Loc 153	91.4	0.73	0.17	-	4.4	21
Loc 153	85.8	0.8	0.17-0.20	-	4.3	21
Loc 153	94.3	0.8	0.17	-	4.3	21
Loc 167	79.2-110	0.4-0.67	0.23	-	4.3	21
Loc 167	86	0.53	0.23	-	4.3	21
Velarifictorus lengwe						
Loc 162	114-165	0.94	0.07	-	6.1	23
Loc 162	118	1.1	0.15	-	6	23
Loc 162	144	1.02	0.08	-	5.7	23
Loc 162	121	1.45	0.10-0.11	-	5.3	23
Loc 170	125	1.23	0.08	-	6.5	27
Loc 170	124	0.77	0.07	-	6.5	27
Loc 170	120	-	-	-	5.3	27
Loc 170	132	-	-	-	6	27
Loc 170	132	-	-	-	6	27
Loc 170	132	-	0.08	-	6.4	27
Loc 170	126	1.9	0.09	-	6	27
Loc 170	115	1.04	0.07	-	6.2	24
Modicogryllus mulanje						
Loc 171	90.7	2.1	0.2	-	5	23
Loc 171	92.8	2.1	0.2	-	4.9	23
Modicogryllus conspersus						
Loc 171	122	3.6	0.13-0.15	-	6.5	23
Loc 171	124	3.6	0.14	-	7	23
Loc 171	161	4	0.11-0.12	-	7.2	23
Loc 171	154	-	-	-	7	23
Loc 171	156	4.3	0.11	-	7.2	23
Loc 171	156	4.2	0.11	-	7	23
Modicogryllus geonomes						
Loc 162	183	37.7	(3-4)	-	6.9	25.5

154, Malawi, 8 km W of Dedza.
155, Malawi, Kasungu National Park
160, Malawi, Viphya Highlands, 12 km S Mzimba.
162, Lake Malawi, at Cape Maclear.
167, Malawi, Michiru Mountain, 8 km NW of Blantyre.
170, Malawi, Lengwe National Park.
171, Malawi, Mulanje Massif, west face.

thirds length of forewings. *Abdomen:* variegated light and dark brown on dorsum, ivory on venter. *Cerci*: pale but covered with dark bristles. *Fore- and midlegs*: ivory colored but with small black spots and larger brownish areas at distal end. *Hind legs:* very pale with a brown area on the inner face of each and with indistinct yellowish oblique stripes on the outer face.

SONG. A sequence of short chirps with a rapid pulse rate.

HABITAT. Thorn bush. Males were found under logs and leaf litter on the surface of the ground.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratypes:* 2M same data as holotype, PHILADELPHIA & PRETORIA.

Velarifictorus viphius n. sp.

TYPE. *Holotype M,* Malawi, Viphya Highlands, 12 km south of Mzimba, 1500 m, 21 iii 1986 (Otte & Glenn 160). PHILADELPHIA.

RECOGNITION. Figs. 15, 17B, 18B. Tables 5, 6. Body color rusty brown on dorsum, blackish on sides and pale on venter with spotted legs. *Head:* dorsum rusty red from vertex to occiput and slighly banded, black from vertex to front of head but with wide white band connecting lateral ocelli; face black above clypeus, very pale on clypeus and labrum; cheeks black. *Pronotum:* dorsum rusty red, somewhat spotted; lateral lobes entirely black. *Forewings:* dorsum brown with some pale veins in apical area; lateral field dark brown to black. *Hindwings:* hidden, about two-thirds length of pronotum. *Abdomen:* dorsum dark brown to black; venter pale brown. *Front legs:* femora mostly very pale but with numerous small black spots and large washes of dark brown on inner and outer faces near distal end and with a black ring at proximal end; tibiae dark brown on loser face, and with dark spots on remainder. *Midlegs:* similar to front legs. *Hindlegs:* femora reddish-brown on upper face, with distinct dark brown oblique stripes on outer face, especially in distal two-thirds; tibiae brown, black at base of each spur.

SONG. A sequence of double pulse chirps.

HABITAT. Miombo woodland, males were singing on the ground under stones.

SPECIMENS. *Holotype* M, PHILADELPHIA.

MODICOGRYLLUS Chopard

Modicogryllus mulanje n. sp.

TYPE. *Holotype M,* Malawi, Mulanje Massif, west face, ca. 1000 m, 30 iii 1986 (Otte, Glenn, & Ruffin 171). PHILADELPHIA.

RECOGNITION. Figs. 16, 17I, 19D. Tables 5, 6. Most similar to *maliensis*, *vittatifrons* and *zinzilulans*, but differing in shape of male epiphallus (see Otte & Cade 1984, fig. 11). Body color dark brown to black on dorsum, but dorsum of head and pronotum with pale marks.

Head: vertex and occiput with six ivory stripes; forehead black but with distinct pale stripe connecting lateral ocelli; face black down to middle of clypeus and with pale area around median ocellus and descending from this a thin pale streak; cheeks black posterior to upper half of eyes and below eyes, otherwise ivory colored. *Pronotum*: dorsum variegated dark brown and ivory; lateral lobes blackish in upper half, ivory in lower half. *Forewings*: dorsal field dark brown; lateral field dark brown above, becoming gradually lighter ventrally. *Abdomen*: tergum black; venter ivory. *Fore- and midlegs*: femora ivory colored but with dark brown at distal end on inner and outer faces; tibiae ivory but with dark brown at proximal end. *Hind legs:* femora with brown oblique stripes on distal half of outer face; dorsal face with large pale area about one tibial diameter anterior to knee; tibiae pale brown but with dark brown streak along ventral face and with dark brown areas at bases of subapical spurs.

SONG. Fig. 2. A rapid succession of short chirps with a very rapid pulse rate.

HABITAT. This species was heard only in grassy clearings near the base of Mount Mulanje in southern Malawi.

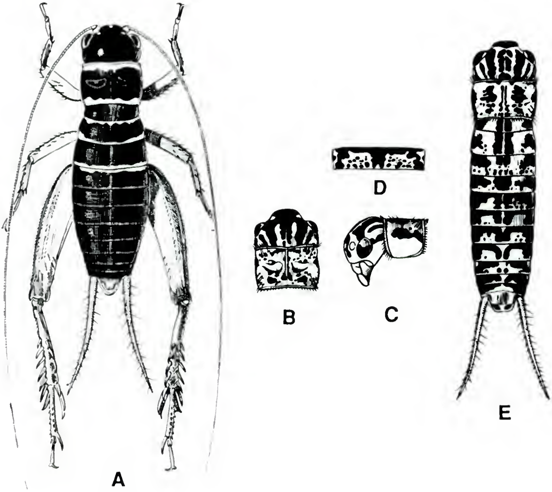


FIG. 20. *Cophogryllus*. **A**, *eshowensis* male; **B**, *maculatus*; **C**, *simonsi* side of head and pronotum; **D**, *simonsi* female abdominal tergite; **E**, *simonsi* male.

COPHOGRYLLUS Saussure

TYPE SPECIES: *Cophogryllus delalandi* Saussure 1877: 232, by subsequent designation, Kirby 1906, v. 2: 44.

Chopard (1967: 37) lists 27 species of *Cophogryllus*. According to his scheme the genus ranges from southern Africa to southeast Asia, and he even includes one species from Peru! Since the genus was defined almost solely by the complete absence of wings, nearly all gryllines which display this character were placed here. It is certain, however, that winglessness evolved many times in the Gryllinae and that few of the species previously assigned to the genus are related to the type species in southern Africa. In previous papers in this series (Otte and Cade 1984a: 96; 1984b: 118) *royi* and *camerunensis* were moved to the genera *Modicoides* and *Sigagryllus* respectively.

The status of this genus remains unclear because the female type from "Afrique méridional" (Paris Museum) and a male "paratype" from unknown locality (Halle Museum) cannot be assigned with certainty to any subsequently collected specimens. However, both Chopard (1955) and Randell (1964) illustrated males (belonging to the same species, it appears) which they called *delalandei*. These illustrations, of the genitalia, the only features which can reasonably be used to define the genus, are figured here. The definition of the genus is here based on those illustrations.

RECOGNITION OF GENUS. A diagnosis for the genus as a whole is not easy to construct because the genitalia are so variable. This may be attributable to the fact that the males are mute and hence may have undergone the kinds of selection pressures which other insects without courtship experience, namely the genitalia become much more species specific than in the case in related groups which have maintained elaborate courtship behavior (Otte 1970). The genus will probably be broken down further as more species become available and the clusters of species become apparent. For the time being we are lumping all species from South Africa which have the following features: both sexes without any trace of forewings; foretibiae without tympana; body shape similar to *Modicogryllus;* color patterns similar to *Modicogryllus*; genitalia variable but usually with the following characteristics: epiphallus broad, with two lateral lobes and and median groove or cleft; ectoparameres highly variable in shape; virga often thick; female ovipositor longer than hind tibiae. All of the species included in the genus are illustrated below and the reader can see for himself the extent of variation and the probable need for future reevaluation.

BIOLOGY. The members of this genus usually are found in exposed areas, in grasslands, and on dry stony hillsides, but they may also occur in wooded areas. We have found no species in heavily forested places. Males and females are found walking about on the ground after dark, or hidden under stones and logs during the day. We have successfully collected them along oatmeal trails in the Cape Province.

Cophogryllus delalandei Saussure

Cophogryllus delalandei Saussure 1877: 234. Type F, Afrique méridionale. PARIS. Type not examined.

The male genitalia of what was thought to be this species were illustrated by both Chopard (1955) and Randell (1964) both from specimens from southern Africa. The description of this species is based upon a female from Afrique méridionale. These are figured below.

Cophogryllus fasciatus Walker

Cophogryllus fasciatus Walker 1869: 50. Type M, Natal. LONDON. Type examined.

The male genitalia of a male presumed to be the type from the British Museum are illustrated below. They are most similar to *maculatus* and *simonsi* (Figs. 2I-K).

Cophogryllus maculatus Chopard

Cophogryllus maculatus Chopard 1955: 293. *Holotype M,* South Africa, Cape Province, Groot Rivier, 12 miles NE Plettenberg Bay, 11 i 1951 (Brinck-Rudebeck). LUND. Type examined.

NOTES ON HOLOTYPE. Figs. 20B, 21A-D, 22AC. Table 7. Variegated with blackish and ivory on dorsum, ivory on venter. *Head:* dorsum dark brown to blackish, with 6 longitudinal stripes on vertex; stripes 1, 2, and 3 distinct on vertex; forehead without pale stripe connecting laterall ocelli; face with large pale area around median ocellus and with an inverted V-shaped ivory band descending from it; cheeks pale, but with a black band from the dorso-posterior marking of the eye to the pronotum. *Pronotum:* widens anteriorly; dorsum with blotchy black markings on a pale brown background; lateral lobes with a black band along the top third, ivory in bottom two thirds. *Abdomen:* dorsum spotted with black markings, largest markings are near center line and on lateral faces of tergites; venter ivory colored; subgenital plate very large. *Front and middle legs:* pale brown to ivory, with small black spots where bristles emerge. *Hindlegs:* femora with rows of dark brown oblique stripes on outer faces, more spotted on upper and inner faces; tibiae dark brown.

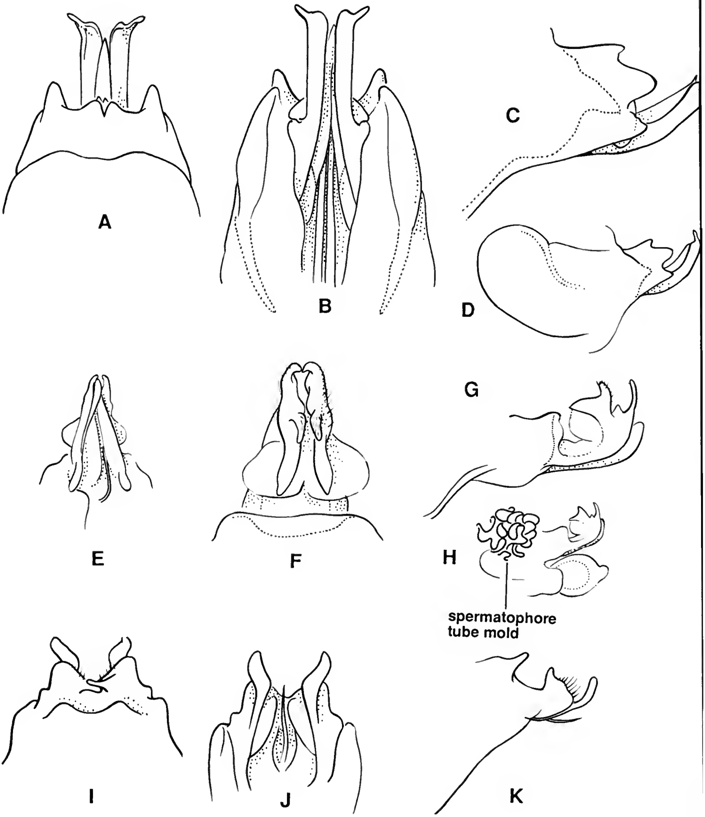


FIG. 21. *Cophogryllus* male genitalia (dorsal, ventral, and lateral views). **A-D**, *maculatus* (not holotype); **E-H**, *simonsi* holotype. **I-K**, *fasciatus* holotype.

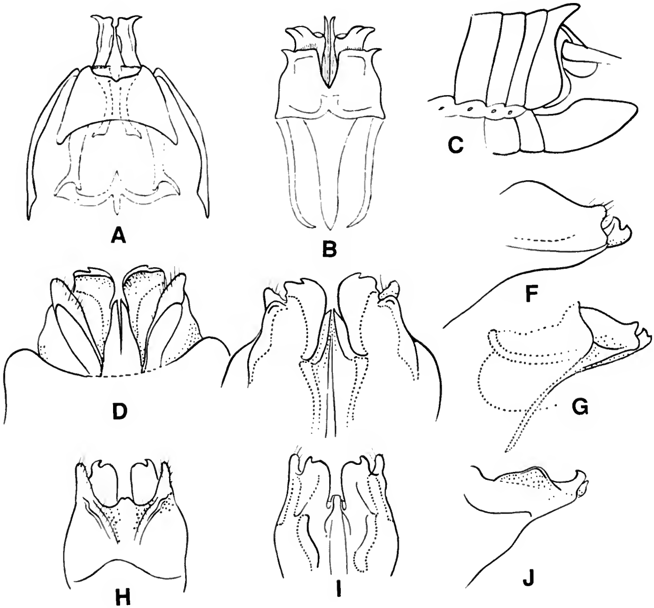


FIG. 22. *Cophogryllus* male genitalia (dorsal, ventral and lateral views). A, *maculatus* (after Chopard 1955: 940); B, *delalandei* (after Chopard 1955: 940); C, *maculatus* showing extended tergum; D-G, *eshowensis* holotype; H-J, *ecourtensis* holotype.

Cophogryllus simonsi n. sp.

TYPE. *Holotype* M, South Africa, Cape Province, Cape Peninsula, above Simonstown, 9 iii 1982 (Otte & Cade 43). PHILADELPHIA.

RECOGNITION. Figs. 20CDE, 21E-H. Table 7. Differs from *maculatus* principally in the male epiphallus.

Males: dorsum strongly patterned with dark brown and ivory, venter pale. *Head:* dorsum with 6 longitudinal stripes and very thin median pale line; two median stripes connected to one another; face pale below median ocellus, cheeks pale. *Pronotum:* dorsum variegated dark brown and ivory; lateral lobes mostly white with dark dorsal stripe. *Mesonotum and metanotum* with two median dark bands and two lateral bands. *Abdomen:* dorsum with regular pattern—two median dark bands and lateral dark areas. *Legs:* pale. *Hindfemora:* pale on outer face with brown oblique stripes which join to form a solid brown band, this dark area extends onto upper and inner

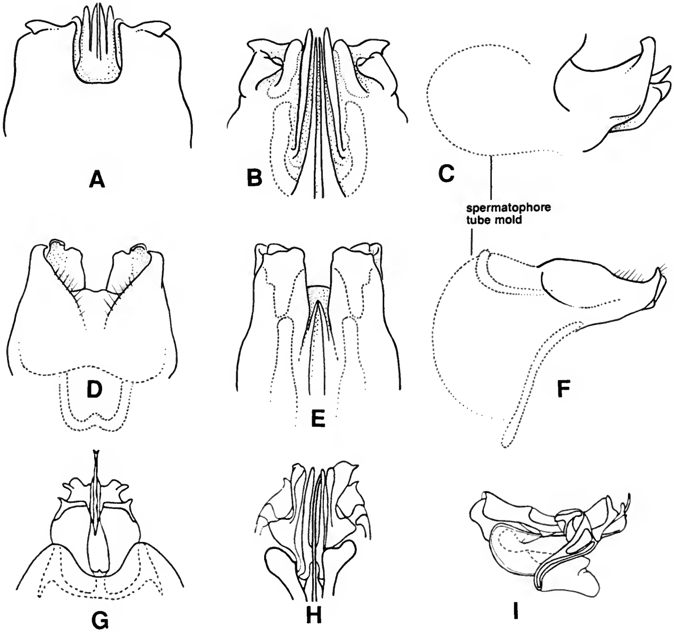


FIG. 23. *Cophogryllus* male genitalia (dorsal, ventral and lateral views). **A-C**, *zoutpansbergi* holotype; **D-F**, *trichardti* holotype; **G-I**, *delalandei* (from Randell 1964).

faces; knees preceded by inner and outer brown patches.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratypes:* same data as holotype, 1F; Loc. 41, 2F (PHILADELPHIA) Determination of latter uncertain, they look like *simonsi* in color pattern.

Cophogryllus eshowensis n. sp.

TYPE. *Holotype M*, South Africa, Natal, 30 km NE of Eshowe, 18 iii 1982 (Otte & Cade 57). PHILADELPHIA.

RECOGNTION. Figs. 20A, 22D-G. Table 7. Differs from other species in configuration of male genitalia and in color: Body color dark red brown and black with orange legs and with strong white bands across thoracic and anterior abdominal segments.

Males: Head: dorsum shiny, very dark red-brown (nearly black); without stripes and without pale interocellar band; face dark red-brown (nearly black) becoming orange on clypeus;

TABLE 7. Species measurements (for abbreviations see Table 1).

	No. file teeth	BL	FL	CL	FWL/PL	TL/FL	OL/FL	Tymp	sub-apical spurs
Cophogryllus simonsi									
HM	-	15.5	8.5	6	-	0.67	-	-/-	4/5
PF	-	19	11	8.2	-	0.74	1.6	-/-	5/5
Cophogryllus maculatus									
HM	-	17	9	-	-	0.71	-	-/-	5/5
PF*	-	15	10	-	-	0.7	1.3	-/-	5/5
Cophogryllus eshowei									
HM	-	15.6	8.5	5.8+	-	0.7	-	-/-	5/5
PM/57	-	14	8.6	-	-	-	-	-/-	5/5
PF/63	-	15	9.3	8.1	-	0.72	0.78	-/-	5/5
PF/57	-	16	9.3	8.9	-	0.75	0.77	-/-	5/5
PF/57	-	15.3	10	-	-	-	0.85	-/-	5/5
Cophogryllus escourti									
HM	-	9.3	5.1	-	-	0.7	-	-/-	4/4
PF	-	10	5.4	4.6	-	0.68	0.8	-	3/4
PF	-	11	5.8	-	-	0.69	0.81	-/-	4/5
PF	-	11	5.8	5	-	0.71	0.8	-/-	4/5
PF	-	10.5	5.7	-	-	-	0.89	-/-	4/5
PF(1)	-	11.5	5.5	-	-	-	0.86	-/-	4/4
PF(1)	-	10	-	-	-	-	0.72	-/-	4/4
Cophogryllus trichardti									
HM	-	10.3	6.7	5.2	-	0.7	-	-/-	5/4,5
PF	-	15	9.4	-	-	0.74	1.06	-/-	5/5
PF	-	12.2	7.4	-	-	-	1.08	-/-	5/4
Cophogryllus zoutpansbergi									
HM	-	12	7.2	5.8	-	0.64	-	-/-	5/5
Cophella macrocephala									
HM	-	19	10.5	6.4	-	0.66	-	-/-	6/6

(1)Little Berg

cheeks black behind top of eyes, becoming orange ventrally. *Pronotum:* dorsum very dark red-brown (nearly black), but white along anterior and posterior margins; lateral lobes pale around anterior, posterior and lower margins. *Mesonotum* with dark posterior margin. *Metanotum* with a pale band along posterior margin. *Abdomen:* dorsum dark red-brown; venter very pale, slightly orange. *Fore- and midlegs:* femora orange brown with stout brown bristles. *Hindlegs:* femora orange brown becoming dark red brown on knees; tibiae red brown.

Females: very similar to males.

HABITAT. Collected along oatmeal trails laid along forest footpaths in a tall natural forest.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratypes:* (PHILADELPHIA) same data as holotype, 1M 2F; Natal, Hluhluwe Game Reserve, 1F.

Cophogryllus escourtensis n. sp.

TYPE. *Holotype M*, South Africa, Natal, 75 km WSW Escourt, 1860 m, Cathedral Peak Forestry Station, 13-31 xii 1979 (S & J Peck). PHILA.

RECOGNITION. Figs. 22H-J. Table 7. Differs from *eshowensis* in the male genitalia, in size and in coloration; metanotum and first abdominal tergite without pale posterior margin.

Males: dorsum very dark red brown (nearly black), with small red median ocellus; face very dark, orange below epistomal suture; cheeks largely dark brown but becoming orange at lower margin of eye. *Pronotum:* dorsum distinctly lighter than head and abdomen; lateral lobes dark brown with pale lower and anterior margins. *Abdomen:* dorsum dark red brown; may be somwhat speckled in females, i.e. lighter brown at posterior margin of tergite with row of darker spots. Cerci brown. *Fore- and midegs:* femora brown, becoming darker distally, with pale spots; tibiae brown. *Hindlegs:* femora: upper outer face with distinct brown oblique stripes; upper face brown with pale spots; knees dark brown, crescent black; tibiae dark brown.

Females: Similar to males but abdomen more strongly variegated with pale and brown.

HABITAT. Evidently collected montane forest floor.

SPECIMENS. *Holotype* M , PHILADELPHIA. *Paratypes:* Same data as holotype, 4F; Little Berg, 1860 m, pan trap, 2F, PHILADELPHIA.

Cophogryllus trichardti n. sp.

TYPE. *Holotype M,* South Africa, Transvaal, Louis Trichardt, Hanglip Plateau, U343, 9 xii 1984 (R. Toms). PRETORIA.

RECOGNITION. Figs. 23D-F. Table 7. Differs from sympatric *zoutpansbergi* in body color and shape of male epiphallus.

Males: Dorsum of body dark reddish-brown to black; venter pale; legs pale but with black markings. *Head:* dorsum shiny black, smooth; with 3 ocelli; face black above middle of clypeus, pale brown below; cheeks dark brown to black dorsally. *Pronotum:* dorsum dark brown, generally lighter toward midline, with thin median pale streak, dark along posterior margin, muscle attachment plates clearly defined and pale brown; with pale areas posterior to muscle attachment plates which have round black spots; lateral lobes black above, pale below, pale area wider anteriorly than posteriorly, lower edge black. *Mesonotum:* central third is dark brown to black (but with median pale streak); lateral to the central dark area are two pale marks, outside of which tergite becomes black. *Metanotum:* mostly reddish brown on dorsum, turning black on sides, posterior margin with two large black areas, one on either side of pale streak along midline; paler areas have black spots. *Abdomen:* covered with fine hairs, dorsum reddish brown, black along posterior margins; venter pale. *Fore- and midlegs:* femora: outer faces pale but with dark brown streak long lower distal part and along distal margin; inner face with several poorly defined dark brown markings near distal end; upper face with black spots, emerging from them are large black bristles; tibiae medium brown. *Hindlegs:* femora: outer faces with oblique dark brown streaks in upper two-thirds, these becoming darker distally; mostly black adjacent to knees; upper face dark brown through most of distal half, but with one large pale patch about two tibial diameters from end of femora and with row of smaller pale spots anterior to that; crescent of knees black centrally, surrounded by pale brown coloration; tibiae medium brown.

Females: Similar to males, but abdomen lighter and more spotted on dorsum—each abdominal tergite with a poorly defined central dark patch, with several horizontal transverse rows of darker spots, larger ones along posterior margin, with large dark patch at shoulder of tergite and horizontal dark streak on other side.

SPECIMENS. *Holotype* M, PRETORIA. *Paratypes:* Hanglip Forest, Louis Trichardt, U344, 10 xii 1984 (R. Toms) 2F, PRETORIA.

Cophogryllus zoutpansbergi n. sp.

TYPE. *Holotype M,* South Africa, Transvaal, Zoutpansberg, Wyliespoort, 8 xii 1984 (R. Toms). PRETORIA.

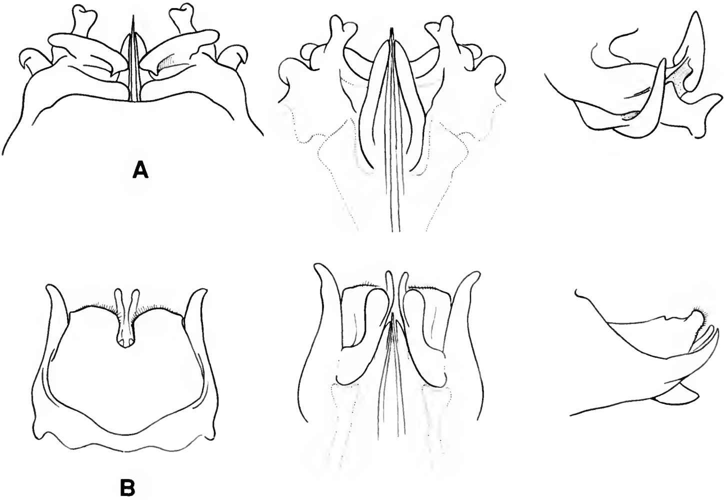


FIG. 24. Male genitalia (dorsal, ventral and lateral views). **A**, *Monbasina rufulus* holotype; **B**, *Nimbagryllus lamottei* holotype.

RECOGNITION. Fig. 23A-C. Table 7. Differs from other species mainly in male epiphallus, and from sympatric *trichardti* in color as well: body color orange-brown, but dorsum of abdomen dark reddish-brown.

Males: Head: dorsum uniform orange-brown, with 3 ocelli; face pale yellowish from middle of clypeus down; cheeks orange, eyes black. Head slighly wider than pronotum. *Pronotum:* dorsum and lateral lobes uniformly orange, with fine dark setae; anterior and posterior margins with black bristles. *Mesonotum* and *metanotum* dark brown like abdominal tergites. *Abdomen:* dorsum dark brown, turning somewhat lighter toward sides, with narrow pale median stripe; venter very pale; cerci pale brown with small dark bristles. *Fore- and midlegs:* femora ivory to yellow-orange. *Hindlegs:* femora orange turning yellow ventrally; tibiae orange.

Females not known.

SPECIMENS. *Holotype* M, PRETORIA.

MOMBASINA n. gen.

TYPE SPECIES. *Mombasina rufulus* (Chopard).

RECOGNITION OF GENUS. The male genitalia which are quite unlike those of the type species of *Oligachaeta* (*O. chabanaudi*). It is therefore

TABLE 8. Species measurements (for abbreviations see Table 1).

	No. file teeth	BL	FL	CL	FWL/PL	TL/FL	OL/FL	Tymp	sub-apical spurs
Astrupia rufa									
HM	105	19.5	9.8	8.2	2.1	0.62	-	-/O	5/5
PM	-	18	10.3	8.3	2	0.65	-	-/O	5/4,5
PM	97	16	9.5	8	2.2	-	-	-/O	5/5
PM	100	15.5	9.5	8	2.1	-	-	-/O	5/5
Astrupia sodwanensis									
HM	76	16	8.2	ca. 7	2.44	0.59	-	-/O	6/6
PM	74	14	8.1	6.5	2.67	0.6	-	-/O	4/5
PM	76	15	7.9	6.3	2.63	0.57	-	-/O	5/5
PM	-	15	7.5	6.3		0.65	-	-/O	-
Cophella macrocephala									
HM	0	19	10.5	6.4	-	0.66	-	-/-	6/6
Nimbagryllus lamottei									
HM	?	14	10	-	1.5	0.8	-	-/O	5/5
MHM	151	14	8	7	2.9	0.8	-	i/O	6/7

placed into a new genus. The forewing venation suggests that this genus is most closely related to *Modicogryllus*. See also *M. rufulus* below and Table 6.

Mombasina rufulus (Chopard)

Gryllus rufulus Chopard 1932 (1934): 335. *Holotype M*, Kenya, Ile de Mombasa, x 1911 (Alluaud & Jeannel). PARIS. *Oligachaeta*, Chopard 1967: 88. Type examined. NEW COMBINATION.

NOTES ON HOLOTYPE. Figs. 24A-C, 29G. Table 8. Small, reddish on dorsum and sides, orange on venter. *Head:* dorsum orange brown; with three ocelli, arranged in triangle; face and cheeks orange brown. *Pronotum:* with parallel sides; dorsum dark brown; lateral lobes dark brown becoming pale in lower anterior corner. *Forewings:* dorsum light brown; lateral field dark brown. *Hindwings:* 1.5 times as long as pronotum. *Abdomen:* dorsum orange brown; venter lighter. *Fore- and midlegs:* unicolorous orange brown. *Hindfemora:* upper and posterior two-thirds dark brown; knees lighter; lower and anterior third orange to yellow.

NIMBAGRYLLUS n. gen.

TYPE SPECIES. *Nimbagryllus lamottei* (Chopard)

RECOGNITION OF GENUS. Differs from all other genera in male genitalia (Fig. 1). Forewings similar to *Mombasina rufulus*; with two harp veins; mirror with one dividing vein. See also *N. lamottei* below.

Nimbagryllus lamottei Chopard

Gryllopsis lamottei Chopard 1954: 68. *Lectotype M*, Guinea, Nimba, Yalahzou, ii-iv 1942 (Lamotte). PARIS. Type examined. NEW COMBINATION.

NOTES ON LECTOTYPE. Fig. 24D-F. Table 8. Body color rusty red, somewhat shiny on head and pronotum. *Head:* dorsum uniformly reddish above mouthparts and epistomal suture, with large ocelli, these not arranged in a line. *Pronotum:* uniformly rusty red. *Forewings:* with very short apical area. *Abdomen:* reddish. *Legs:* all uniformly reddish. Basitarsus on foreleg not different from that on middleleg, hence not brachytrupine in nature.

Table 9. Songs of *Astrupia* species. (See table 8 for key to abbreviations).

	p/s	ch/s	chirp length in seconds (or p/ch)	KHz	°C
Astrupia gazensis					
Loc 20	44.0		0.61	5.8	25
Loc 20	44.0	0.92	0.64	5.8	25
Loc 20	44.0	0.90	0.57-0.70	6.0	25
Astrupia sodwanensis					
Loc 178	88	1.94	(11-12)	5.2	80
Loc 178	85	2.54	(11-12)	4.9	80
Loc 178	85.8	2.11	(11-14)	5.0	80

ASTRUPIA n. gen.

TYPE SPECIES. *Astrupia gazensis* n. sp.

This genus, represented by two species has been collected only in northern Zululand in sandy habitats. The type species was found in thornbush in the Mkuze Game Reserve, and *sodwanensis* was found in rolling sand dunes just inland from the tall coastal dunes at Sodwana Bay. Quite possibly the genus extends northwards into Mozambique.

RECOGNITION OF GENUS. Differs from all other genera in configuration of genitalia. Epiphallus in type species is so unique that I cannot match it with that of any other genus; therefore placement with Modicogryllini is tentative.

Astrupia gazensis n. sp.

TYPE. *Holotype M*, South Africa, Natal, Mkuze Game Reserve, 19 xi 1980 (D. Otte 20). PHILADELPHIA.

RECOGNITION. Figs. 25A, 26, 27A-D, 29E. Tables 8, 9. Generally most similar to *Acheta* in appearance, but differing from that genus and all others by male genitalia.

Males: Body color orange brown to reddish on dorsum; very pale on venter and legs. *Head:* dorsum orange to reddish, without pale stripes; face very pale below median ocellus; cheeks pale below middle of eyes. *Pronotum:* pubescent; dorsum orange to yellow; slightly variegated; orange through most of central part, becoming very pale towards margins; lateral lobes with sinuous brown band along top, ivory below; with dense reddish fringe of hairs along anterior and posterior margins. *Forewings:* dorsum red brown, becoming ivory towards lateral margins; lateral field very pale; dark red-brown between upper three veins. *Hindwings:* absent. *Abdomen:* dorsum red brown, banded each tergit becoming pale on side of body; venter very pale. *Fore- and midlegs:* pale straw-yellow; tibiae with very longitudinal thin apical spurs, longest almost as long as basitarsus. *Hindfemora:* darker red around knees, with dense reddish or golden setae.

HABITAT. Collected in thorn savanna. Males were found singing on small bushes in a sandy area surrounded by thorn trees.

SONG. Short trills. Most males were singing from the stems of bushes and trees up to meter above the ground.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratypes*: 3M same data as holotype, PHILADELPHIA & PRETORIA.

Astrupia sodwanensis n. sp.

TYPE. *Holotype M*, South Africa, KwaZulu, Sodwana Bay, heath zone west of beach, 10 iv 1986 (Otte and Glenn 178). PHILADELPHIA.

RECOGNITION. Figs. 25B, 26, 27E-G, 29F. Tables 8, 9. Differs from *gazensis* as follows: dorsum of head with very distinct longitudinal

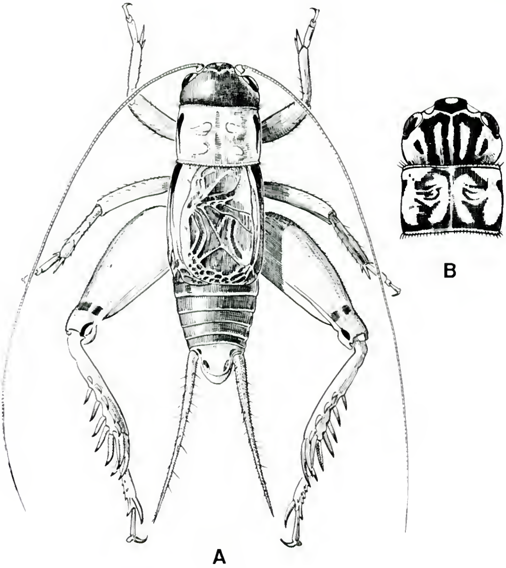


FIG. 25. A, *Astrupia gazensis*; B, *Astrupia sodwanensis*.

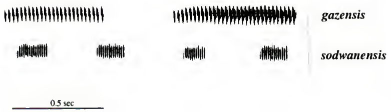


FIG. 26. *Astrupia* songs from type localities.

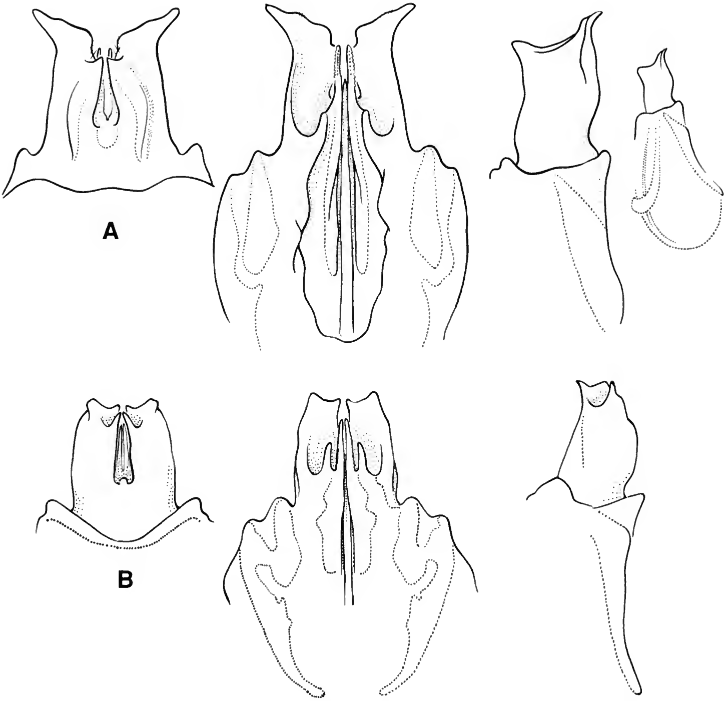


FIG. 27. *Astrupia* male genitalia (dorsal, ventral and lateral viewe). **A**, *gazensis* holotype; **B**, *sodwanenesis* holotype.

light and dark bands on vertex and occiput; dorsum of pronotum variegated; genitalia as figured; much smaller (see table of comparison); song as figured.

Body color variegated light and dark brown on dorsum and pale on the sides and venter. *Head*: vertex and occiput with six light and six dark stripes, rostrum dark brown, but with large pale area surrounding median ocellus; face almost entirely pale but with dark streaks along upper edges of antennal sockets; cheeks entirely pale. *Pronotum*: dorsum variegated light and dark brown as in figure; lateral lobes ivory, but with narrow dark band along the top. *Forewings*: dorsal field brown; lateral field pale, but with a brown band along upper two veins. *Hindwings*:

absent. *Abdomen*: dorsum dark brown, but last two segments largely pale except for several dark markings on either side. *Fore- and midlegs*: femora very pale with wash of brown on inner and outer faces near distal end. *Hindlegs*: femora very pale, outer face with oblique light gray stripes; tibiae pale brown, spurs very long and with setae.

SONG. A train of long chirps (or short trills).

HABITAT. This species lives in burrows in sand dunes covered with grass and heath. All males were found singing at the entrance to a burrow.

SPECIMENS. *Holotype* M PHILADELPHIA. *Paratypes:* 3M, same data as holotype, PHILADELPHIA and PRETORIA.

COPHELLA n. gen.

TYPE SPECIES. *Cophella macrocephala* n. sp.

RECOGNITION OF GENUS. Differs from all other genera in configuration of the male genitalia, Fig. 29. Head extremely large; pronotum much wider anteriorly than posteriorly. Wings entirly absent and auditory tympana entirly absent. Hind tibiae two thirds as long as hind femora, with six inner and six outer subapical spurs. See also RECOGNITION below.

Cophella macrocephala n. sp.

TYPE. *Holotype M*, Angola, Pico Azevedo, 1200 ft, 8 x 1930 (R. and L Boulton). PHILADELPHIA.

RECOGNITION. Figs. 28, 29A-D. Table 8. Distinguished by very large head and the male genitalia.

Males: medium sized cricket with very large head. Body color dark brown to blackish on dorsum; pale brown to yellowish on venter. *Head:* almost entirely black, becoming red-brown on mouthparts; occiput with fine pubescence; all three ocelli well-developed, nearly equal in size; eyes small. *Pronotum:* much wider at anterior end; almost entirely dark brown but dorsum with reddish muscle attachment plates, and lateral lobes pale along lower anterior margin. *Forewings:* absent. *Abdomen:* dark brown on dorsum; pale brown on venter. *Legs:* all pale brown to orange brown.

SPECIMENS. *Holotype* M, PHILADELPHIA.

INCERTAE SEDIS

SONGELLA n. gen.

TYPE SPECIES: *Songella obscuripennis* (Chopard).

RECOGNITION of GENUS. Differs from similar genus *Callogryllus*, as follows: Venation in mirror and chordal areas strongly modified; mirror absent, diagonal vein nearly obsolete, or fusing with chordal veins; apical area almost without veins; posterior margin of forewings oblique; basal area of forewing relatively large; male epiphallus elongate, truncated at end; virga stout (see also *Parasongella* diagnosis). See also *S. obscuripennis*.

Songella obscuripennis (Chopard)

Callogryllus obscuripennis Chopard 1927: 155. *Holotype M*, Ost Afrika, Tanzania, Dar-es-Salaam (R. Ebner). VIENNA. Type examined.

NOTES ON HOLOTYPE. Figs. 30F, 33A-C. Table 10. Body color black and brown; legs pale brown. *Head:* dorsum dark brown, with six longitudinal stripes; ones behind eyes broadest; face mostly yellow, patterned with dark brown; side of head mostly yellow, but with broad dark band behind upper part of eye. *Pronotum:* disc patterned with pale and dark brown; lateral lobes dark brown in upper two-thirds, pale in lower third. *Forewings:* shorter than pronotum; median pronotal length equal to forewing length.

SPECIMENS. *Holotype* M, VIENNA.

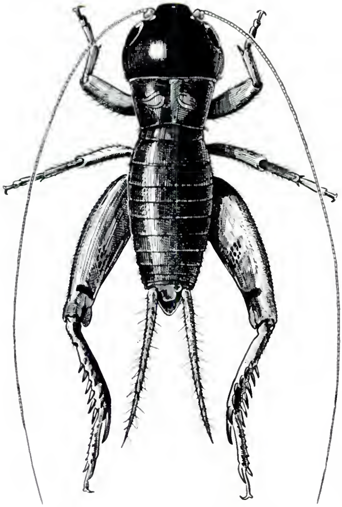


FIG. 28. *Cophella macrocephala* male holotype.

Songella ebneri (Chopard)

Callogryllus ebneri Chopard 1927: 154. *Lectotype M*, here designated, Ost Africa, [Tanzania] Dar-es-Salaam (R. Ebner). VIENNA. Type examined.

NOTES ON LECTOTYPE. Figs. 30G, 33D-F. Table 10. Body color dark brown, but legs pale brown; lower half of lateral lobes and lower half of face pale brown; ocellus large, yellow, not connected with lines. Forewings: very short, about half as longitudinal as pronotum.

Females: entirely wingless.

PARASONGELLA n. gen.

TYPE SPECIES: *Parasongella nigriceps* n. sp.

RECOGNITION OF GENUS. Differs from *Songella* as follows: epiphallus with two pointed lobes; ectoparamere with two narrow processes on either side; virga very wide at base, narrowing suddenly to very narrow elongate process; forewing with well-developed apical area with numerous veins; diagonal vein well-developed; basal area relatively small. See also *S. nigriceps.*

Parasongella nigriceps n. sp.

TYPE. *Holotype M*, Tanganyika Territory [Tanzania], Matengo Highland, WSW of Songea, Ugano 15-1700 m, 11-20 xii 1935 (Zerny). VIENNA.

RECOGNITION. Figs. 30E, 33G-I. Table 10. Distinguished from *ebneri* and *obscuripennis* by the male epiphallus.

Males: Body color black, except bottom of face which is brown. No pale lines connecting lateral ocelli. Median ocellus small. Clypeus bent strongly upwards. *Pronotum:* black, slightly narrower than head, front slightly wider than rear. *Abdomen and legs:* black. *Abdomen:* dorsum (under forewing) with dense mat of long pale hairs (as long as abominal tergite is wide). *Hindwings:* absent.

SPECIMENS. *Holotype* M, VIENNA.

CALLOGRYLLUS Sjöstedt

TYPE SPECIES. *Callogryllus kilimanjaricus* Sjöstedt.

RECOGNITION OF GENUS. Ectoparameres long, hinged at base so that they swing through 180 ; forewings without mirror; chords may be strongly modified so that inner chord connects either with diagonal vein or with stridulum; diagonal vein connects to stridulum rather than to stem of chords. Differs from *Omogryllus* in pos-

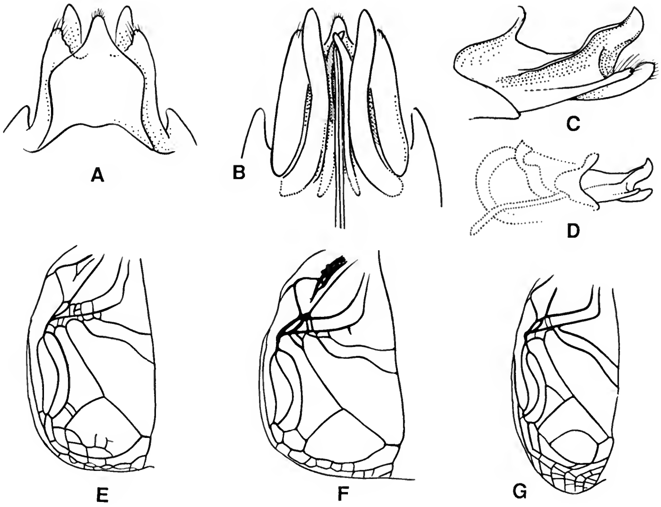


FIG. 29. **A-D,** *Cophella macrocephala* male genitalia; **E,** *Astrupia gazensis* holotype forewing; **F,** *Astrupia sodwanensis* holotype forewing; **G,** *Mombasina rufulus* holotype forewing.

sessing forewings and auditory tympana. See also *C. kilimanjaricus* below.

Callogryllus kilimanjaricus Sjöstedt

Callogryllus kilimanjaricus Sjöstedt 1909, Kilimanjaro-Meru Exp. 3: 105. *Holotype M,* Kilimanjaro, Kibonoto, 1800-1900 m, 1905-1906. STOCKHOLM. Type examined.

NOTES ON HOLOTYPE. Figs. 30B, 31C, 32, 34A-C. Table 10. *Male:* Differs from *parvus* and *olohius* mainly in that it possesses elongate, two-lobed, pointed epiphallus. Small, narrow, dark brown with pale orange legs. *Head:* dorsum dark reddish brown, without stripes; frons wide, ocelli pale, frons with slightly overlapping sides and little groove at level of antennae; clypeus and mouthparts pale yellow-brown; cheeks dark brown behind eyes, gradually fading ventrally. *Pronotum:* dorsum dark reddish brown; lateral lobes with black dorsal band, ivory lower band and black edge. *Forewings:* brown, becoming pale at lower side of lateral field. *Abdomen:* dark reddish brown on dorsum, pale brown on venter. *Foretibiae*: with no inner and a large outer tympanum. *Fore- and midtibiae* with 3 and 4 apical spurs respectively. Legs orange-brown. *Hindfemora*: comparatively large.

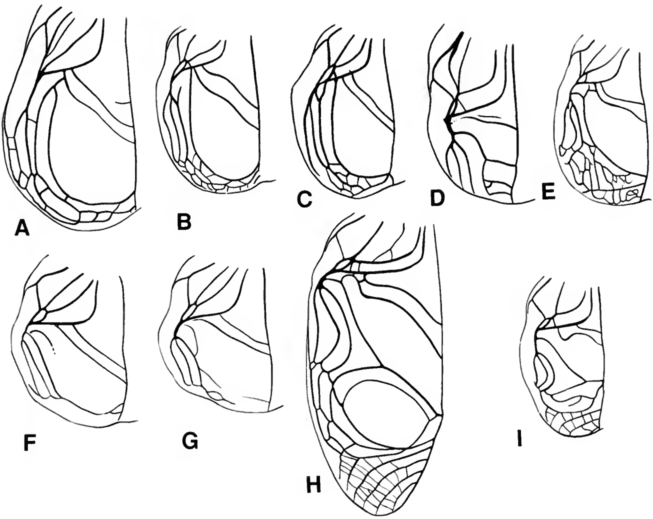


FIG. 30. Male forewings (all of holotypes). A, *Callogryllus parvus*; B, *Callogryllus kilimanjaricus*; C, *Callogryllus olohius*; D, *Grylloderes testaceus*; E, *Parasongella nigriceps*; F, *Songella obscuripennis*; G, *Songella ebneri*; H, *Oligachaeta chabanaudi*; I, *Oligachaeta tripartita*.

Callogryllus parvus Chopard

Callogryllus parvus Chopard 1932 (1934): 338. *Lectotype M*, here designated, Mt. Kinangop, East Africa. PARIS. Type examined.

NOTES ON LECTOTYPE. Figs. 30A, 35D, E. Table 10. *Male:* very small, head and thorax shiny brown, with reddish-brown legs. *Head:* dorsum dark brown to black; face rusty-red below epistomal suture; cheeks dark red-brown, becoming lighter towards mandibles. *Pronotum:* dorsum very dark red-brown, nearly black; lateral lobes like dorsum, but extreme lower front corner pale. *Forewings:* dorsal field red-brown; lateral field black near dorsal edge. *Hindwings:* absent. *Abdomen:* dorsum dark red-brown; venter medium brown. *Fore- and midlegs:* red-brown; tibiae red-brown. *Hindlegs:* femora orange; tibiae orange.

Callogryllus olohius n. sp.

TYPE. *Holotype M*, Kenya, Nairobi, Karen, Olohia Forest, 3 x 1982 (N. D. Jago). PHILADELPHIA.

RECOGNITION. Figs. 30C, 34D-G. Table 10. Differs from *parvus* and *kilimanjaricus* in male genitalia.

Males: Head: dorsum dark brown to black with lighter band extending from back of eye to pronotum; face dark brown above, with pale stripe descending from median ocellus, lightest

TABLE 10. Species measurements (for abbreviations see Table 1).

Species	No. file teeth	BL	FL	CL	FWL/PL	TL/FL	OL/FL	Tymp	sub-apical spurs
Songella obscuripennis									
HM	109	13	9	-	< 1.0	0.91	-	-/-**	5/5
Songella ebneri									
LM	90	13	9.5	7.1	0.5	0.58	-	-/O	5/5
PLF			11	9.1	0	-	0.76	-/O	5/5
Parasongella nigriceps									
HM	57	14	?	?	2	?	-	-/O	?
Callogryllus kilimanjaricus									
HM	—	14	9	-	2	0.71	-	-/O	6/7
Callogryllus olohius									
HM	75	11.5	6.1	5.1	2.2	0.75	-	-/-	5/5
Callogryllus parvus									
LM	48	7.7	5.2	4.2	2.8	0.67	-	-/O	4/4
Omogryllus jeanelli									
HM	-	10	6.2	4.7	-	0.72	-	-/-	4/4
F		12.5	6.8	4.9	-	0.72	1.02	-/-	5/5
Oligachaeta chabanaudi									
HM	??	14.5	9	-	4.3	0.83	-	i/O	6/5
Oligachaeta tripartita									
HM	81	11.5	8	-	2.1	-	-	-/O	5/5
Clearidas nigriceps									
HM	none	15	7	7	3.4	0.8	-	-/O	2,3/3
Grylloderes testaceus									
LM	85	12	?	?	1.15	?	-	-/O	?

* obsolete, but traces remain, covered with seta

on lower lobe of clypeus. *Pronotum:* dark brown to black with pale area at lower anterior corner. *Forewings:* dorsum pale brown; lateral field pale brown, darker near upper margin. *Hindwings:* absent. *Abdomen:* dorsum dark brown; venter pale brown, with median darker brown band; cerci pale brown. *Fore- and midlegs:* femora pale with brown spots on upper face and with larger brown marks at distal end; tibiae brown. *Hindlegs:* femora pale with oblique brown stripes on outer face, these becoming darker distally, darker brown on upper face and with pale spots there; dark brown around knees; tibiae brown.

OMOGRYLLUS n. gen.

TYPE SPECIES. *Omogryllus jeanelli* (Chopard).

RECOGNITION of GENUS. Differs from *Callogryllus* in lacking forewings and auditory tympana; similar genitalia show that these two genera are related. See *O. jeanelli*. See *O. jeanelli* for further description.

Omogryllus jeanelli (Chopard)

Cophogryllus jeanelli Chopard 1938: 128. *Holotype M,* Kenya, Mais Forest, Kinangop,Mt Aberdare, towards West, 2800 m, 1932-1933 (Chappuis and Jeanell). PARIS. Type examined. NEW COMBINATION.

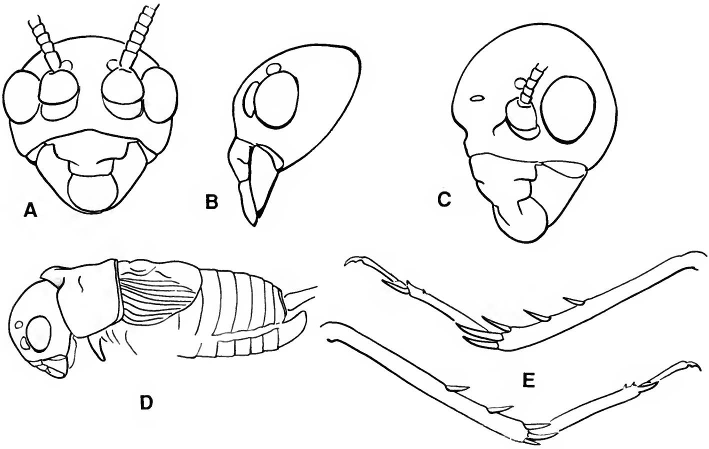


FIG. 31. A, B, *Clearidas nigriceps* holotype; C, *Callogryllus kilimanjaricus* holotype; D, *Grylloderes testaceus* holotype, showing notch and projection at anterior end of pronotum; E, *Clearidas nigriceps* holotype showing inner and outer faces of hind tibiae and tarsi.

NOTES ON HOLOTYPE. Fig. 35A-C. Table. 10. Body very pubescent; dark brown to black on dorsum; brown on venter; legs brown. *Head:* dorsum almost entirely black, but with reddish stripe extending from inner posterior margin of eye to anterior margin of pronotum. *Pronotum:* dorsum largely black but with two pale brown marks at posterior edge, one on either side of midline; these pale marks extending onto mesonotum and metanotum; lateral lobes black, but ivory-colored along lower margin, lower edge black. *Wings:* absent. *Abdomen:* dorsum dark brown to black with some brown spots; venter light brown. *Fore- and midlegs:* light brown becoming dark on upper face and at distal extremity; tibiae brown. *Hindlegs:* femora red brown with dark brown oblique stripes, becoming dark brown on dorsum and towards extremity.

Female: mesonotum and metanotum with two large pale areas, one on either side of midline, and with rows of pale spots on dorsum, thin median line, and two rows of spots on either side of midline.

SPECIMENS. *Holotype* M, PARIS. Same data as holotype, 1F, PARIS.

OLIGACHAETA Chopard

TYPE SPECIES: *O. chabanaudi* (Chopard).

The male genitalia of this species have been illustrated for the first time. They are complex and show no close affinity with any other genus.

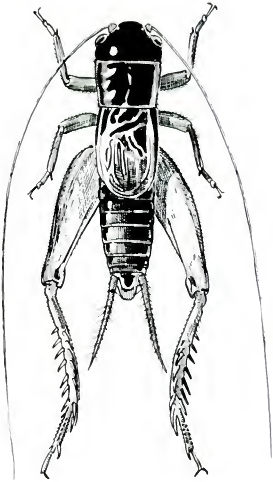


FIG. 32. *Callogryllus kilimanjaricus* male.

Oligachaeta chabanaudi (Chopard)

Gryllus chabanaudi Chopard, 1925: 443. *Holotype M*, Liberia, Rég.de Beyla, April (P.Chabanaud). PARIS. *Acheta*, Ebner, 1931. *Oligachaeta*, Chopard 1961: 275. Type examined.

NOTES ON HOLOTYPE. Figs. 30H, 36, 37A-C. Table 10. Pale orange with relatively very large forewings; general aspect similar to some southeast Asian Itarinae. *Head:* dorsum, face and cheeks unicolorous, pale orange brown; with 3 ocelli. *Pronotum:* dorsum and lateral lobes unicolorous orange brown. *Forewings:* entirely orange brown; harp with 2 veins; mirror once divided. *Hindwings:* extending about 3 pronotal lengths beyond forewings. *Abdomen:* entirely orange brown. *Legs:* all pale orange brown.

Oligachaeta tripartita (Chopard)

Gryllopsis tripartita Chopard 1954: 67. *Holotype M*, Guinea, Nimba, Mt. To, 1600 m, ii-iv 1942 (Lamotte). PARIS. Type examined. NEW COMBINATION.

NOTES ON HOLOTYPE. Figs. 30I, 37D E. Table 10. Body color reddish brown, darkest on head, micropterous. *Head:* dorsum medium to dark brown; face pale brown below median ocellus; cheeks dark brown posterior to tops of eyes, becoming lighter ventrally. *Pronotum:* dorsum brown, slightly ligher on muscle attachment plates; lateral lobes pale brown in lower half, dark brown in upper half. *Forewings:* entirely brown. *Abdomen:* reddish brown, and without distinctive markings. *Legs:* all reddish brown, and without distinctive markings.

GRYLLODERES Bolivar

TYPE SPECIES. *Grylloderes brunneri* Riggio.

We have not seen the type species of *Grylloderes*, known only from Sicily. Whether the two species below belong to this genus will ramain uncertain until the genitalia of *brunneri* are examined. *G. testaceus* and *subalatus* are very different from one another and so are probably not congeneric, but because the type of the latter is a female one cannot tell for sure. And it seems highly unlikely that members of one genus would be collected in southern Europe and central Africa and not in the intervening regions.

Grylloderes testaceus Chopard

Grylloderes testaceus Chopard 1934: 34. *Lectotype M*, here designated, Congo [Zaire], Katanga, Pweto, x 1926 (A. Bayet). TERVUREN. Specimen bears the label *Callogryllus testaceus*.

NOTES ON LECTOTYPE. Figs. 30D, 31D, 38A-C. Table 10. Small orange brown with oddly

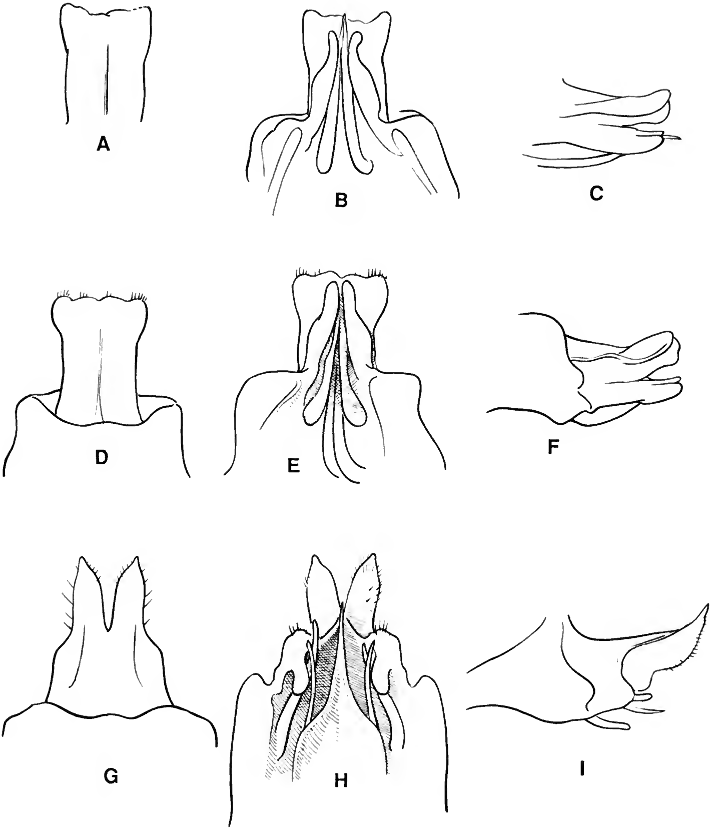


FIG. 33. Male genitalia (dorsal, ventral and lateral views). **A-C**, *Songella obscuripennis* holotype; **D-F**, *Songella ebneri* holotype; **G-I**, *Parasongella nigriceps* holotype.

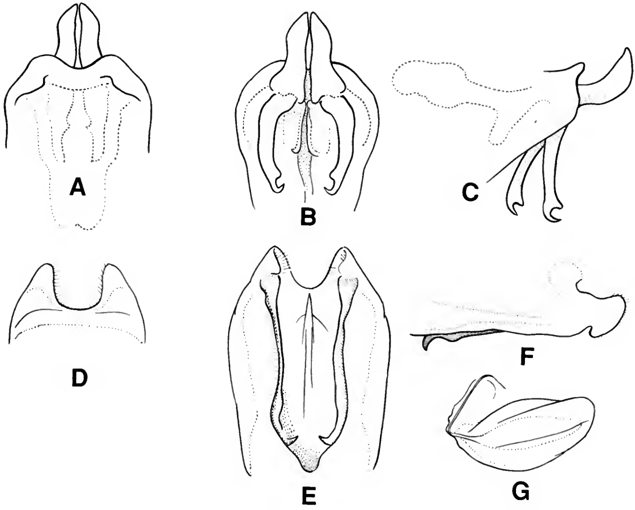


FIG. 34. Male genitalia (dorsall, ventral and lateral views). A-C, *Callogryllus kilimanjaricus* holotype; D-G, *Callogryllus olohius* holotype (G, spermatophore).

shaped pronotum. *Head*: dorsum orange brown; all three ocelli large, yellowish; face ivory-colored below median ocellus and below middle of antennal sockets; mouthparts short. *Pronotum*: dorsum oddly crimped at anterior margin, revealing two holes between pronotal margin and head; dorsal coloration or brown, becoming pale on lateral lobes. *Forewings*: venation around mirror rudimentary, brownish on dorsal field; pale on lateral field, but dark brown along dorsal margin. *Abdomen*: reddish brown. *Legs:* straw colored; fortibiae with only a large outer tympanum; basal tarsomere more than one third length of tibiae. Hindlegs lost.

Grylloderes subalatus Chopard

Grylloderes subalatus Chopard 1951:301. *Holotype* F, Congo, W. Kivu: Kashusha, 1937 (Vandelannoite). Type examined. TERVUREN.

NOTES ON HOLOTYPE. This female is very different in appearance from the male of *testaceus* and it is unlikely that they belong to the same genus. Only dissection of the male genitalia will reveal the true position of *subalatus*. The female is a medium to small brown cricket with shiny dark brown head and pronotum. Top of head without dark or pale stripes. Median ocellus surrounded by large pale area. Face dark brown in dorsal half. Cheeks dark brown. Pronotum

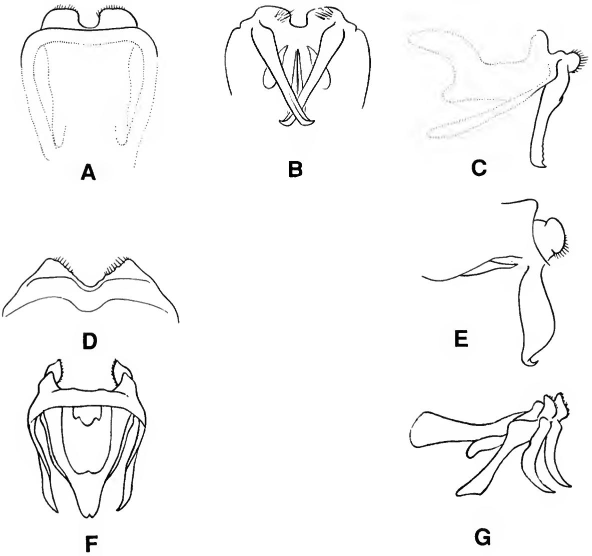


FIG. 35. Male genitalia (dorsal, ventral and lateral views). A-C, *Omogryllus jeanelli* holotype; **D, E,** *Callogryllus parvus* holotype; **F, G,** *Callogryllus parvipennis* (from Chopard).

somewhat variegated light and darker brown; lateral lobes dark brown in upper three quarters, and with light band along lower margin. Dorsum of abdomen lighter brown marbled with darker brown. Forewings about two thirds length of pronotum, triangular in dorsal view, and not overlapping along midline. Foretibiae with large outer and no inner tympanum. All legs reddish brown. Hind tibiae with 5 inner and 5 outer subapical spurs. Body length ca. 13 mm; hind femura length 9 mm; ovipositor length 9 mm.

CLEARIDAS Stål

This genus is unique in possessing only apical spurs on the fore- and midtibiae.

Clearidas nigriceps Stål

Clearidas nigriceps Stål 1876: 64. *Holotype M*, Damara [Botswana]. STOCKHOLM. Type examined.

NOTES ON HOLOTYPE. Figs. 31AB, 31E, 38D-F. Table 10. Top and sides of head dark brown.

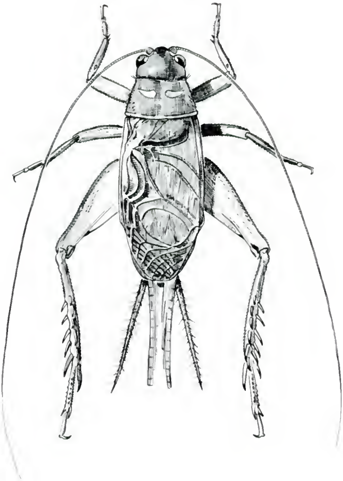


FIG. 36. *Oligachaeta chabanaudi* male.

Pronotum pale yellowish on dorsum, dark brown on sides. *Forewings*: pale straw colored, with straight veins, without a stridulum and mirror. Hindwings: extending almost one body length beyond forewings. Legs yellow. *Abdomen*: dorsum dark brown; venter pale, yellowish. Foretibiae with 2 apical spurs; middletibiae with 2 apical spurs.

ACKOWLEDGEMENTS

I thank my field companions William Cade, George Glenn, and Jane Ruffin for their assistance and good humor. I am especially thankful to the Malawi Department of National Parks and Wildlife for their help and accomodations and to the friendly people of Malawi. I am also indebted to the following museums for sending type and other material for study. Zoologisches Museum, Humboldt-Universität, Berlin; British Museum (Natural History); Zoological Museum, Lund; Muséum d'Histoire Naturelle, Paris; Transvaal Museum, Pretoria; Naturhistoriska Riksmuseet, Stockholm; Musee Royal de l'Afrique Centrale, Tervuren; and Naturhistorisches Museum, Vienna.

LITERATURE CITED

CHOPARD, L. 1925. Liste des Gryllides recueillis par M. Paul Chabanaud en Afrique Occientale. Bulletin Muséum National d'Histoire Naturelle 1925: 442-446.

——— 1927. Descriptions des Gryllides nouveaux. Annales Société entomologique France 96: 147-174.

——— 1932. Voyage de Ch. Alluaud et R. Jeannel en Afrique Orientale (1911-1912). Gryllidae. Eos, Madrid 8: 325-362.

——— 1934. Catalogues raisonnés de la Faune Entomologique de Congo Belge. Orthoptères, Gryllides. Annales du Musée du Congo Belge, Tervuren. Zoologie, Série 3, Section II, 4(1): 1-88.

——— 1938. On a collection of Gryllidae and Tridactylidae from Sierra Leone. Annals and Magazine of Natural History, London (11) 1: 49-66.

——— 1938. Orthoptera. 1. Dictyoptera, Phasmodea, Ensifera. In: Mission Scientifique de'l Omo, 4 (33):

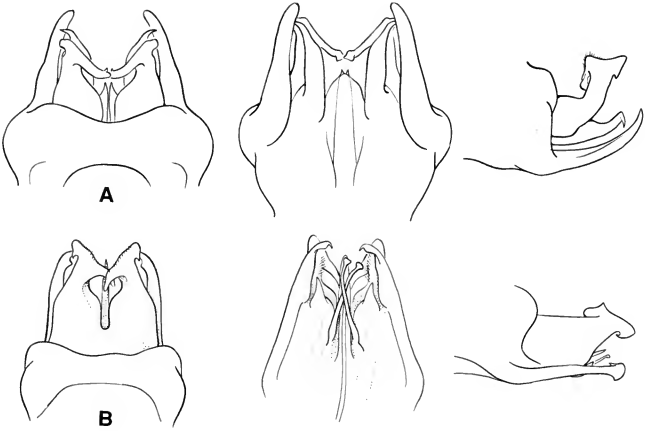


FIG. 37. *Oligachaeta* male genitalia (dorsal, ventral and lateral views). A, *chabanaudi* holotype; B, *tripartita* holotype.

89-134. In: Memoires du Muséum National d'Histoire Naturelle, Nouvelle série, Tome VIII.

——— 1945. Orthopteroides recueillis das les montagnes du Camerun par la mission Lepesme, Paulian, Villiers. Revue Française d'Entomologie 11: 156-178.

——— 1954. La réserve naturelle integrale du Mont Nimba. III. Orthopteres Ensifères. Mémoires de l'Institut français d'Afrique noire, No. 40, fasc. 2: 25-97.

——— 1954 (1955). La réserve naturelle intégrale du Mont Nimba. III. Orthoptères Ensifères. Mémoires de l'Institut français d'Afrique noire, 40, fasc 2.

——— 1955. South African Animal Life. Results of the Lund University Expedition in 1950-1951, vol. 2: 266-301.

——— 1961a. Orthoptères. Gryllidae et Gryllacrididae l'Angola. Companhia de Diamantes de Angola, Publicacoes Culturais 56: 15-69.

——— 1961b. Les division du genre Gryllus basées sur l'étude de l'appareil copulateur (Orthoptera, Gryllidae). Eos, Madrid 37: 267-287.

——— 1967. Orthopterorum catalogus. Pars 10. Gryllides. M. Beier, editor. W. Junk, Gravenhag

Gorochov, A. 1983. To the knowledge of the cricket tribe Gryllini (Orthoptera, Gryllidae. Revue d'Entomologie de l'URSS 62 (2): 314-330.

Karny, H. 1910. G. Orthoptera. In L. Schultze, Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Südafrica ausgeführt in den Jahren 1903-1905. Vierter Band. Systematik und Thiergeographie. Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena, Band 16: 34-90.

Karsch, F. 1893. Die Insekten der Berglandschaft Adeli im Hinterlande von Togo (Westafrica). Entomologisches Zeitschrift 38: 9-266.

Otte, D. 1983. African Crickets (Gryllidae). 2. Afrogryllopsis Randell and Neogryllopsis n. gen. of eastern and southern Africa. Proceedings of The Academy of Natural Sciences of Philadelphia 135: 218-235.

——— 1985. African crickets (Gryllidae: Gryllinae). 7. The genus Cryncus Gorochov. Proceedings of the Academy of Natural Sciences of Philadelphia 137: 129-142.

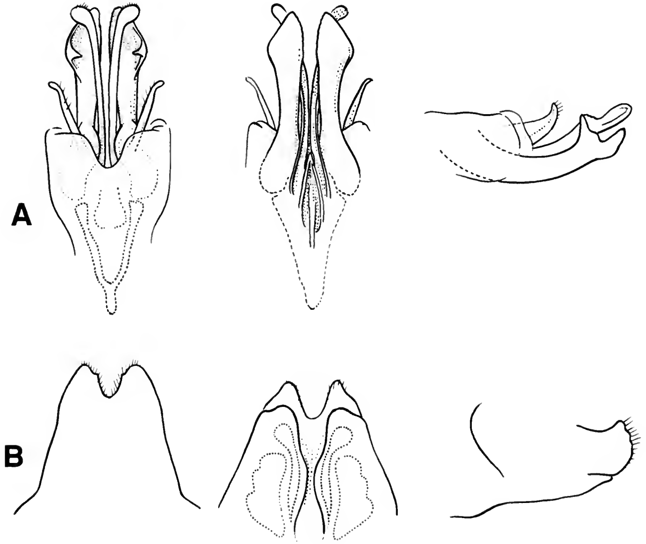


FIG. 38. Male genitalia. **A**, *Grylloderes testaceus* holotype; **B**, *Clearidas nigriceps* holotype.

——— 1985. African crickets (Gryllidae). 8. Further notes on Velarifictorus and other genera. Proceedings of The Academy of Natural Sciences of Philadelphia 137: 143-152.

Otte, D. and W. Cade. 1983a. African Crickets (Gryllidae). 1. Teleogryllus of eastern and southern Africa. Proceedings of the Academy of Natural Sciences of Philadelphia 135: 102-127.

——— 1983b. African Crickets (Gryllidae). 3. On the African species of Velarifictorus Randell (Gryllinae, Modicogryllini). Proceedings of the Academy of Natural Sciences of Philadelphia 135: 241-253.

——— 1984b. African Crickets (Gryllidae). 5. East and South African species of Modicogryllus and several related genera (Gryllinae, Modicogryllini). Proceedings of the Academy of Natural Sciences of Philadelphia 136: 67-97.

——— 1984c. African Crickets (Gryllidae). 6. The genus Gryllus and some related genera (Gryllinae, Gryllini). Proceedings of the Academy of Natural Sciences of Philadelphia 136: 98-122.

Randell, R. L. 1964. The male genitalia in Gryllinae (Orthoptera: Gryllidae) and a tribal revision. Canadian Entomologist 96: 1565-1607.

Saussure, H. de. 1877. Melanges Orthopterologiques. 5me fascicule. III. Gryllides. Mémoires de la Société de Physique et d'Histoire Naturelle de Genève 25: 1-352.

Tarbinsky, S. P. 1940. Pryigayushchiye pryamokriliye nasyekomiye. Azyerbaidjandkoi S. S. R. Moscow and Leningrad.

Sjöstedt, Y. 1909. Kilimanjaro-Meru Expedition 3: 105.

Proceedings of The Academy of Natural Sciences of Philadelphia 139: 375-457, 1987

The Crickets of New Caledonia (Gryllidae)

DANIEL OTTE
Academy of Natural Sciences of Philadelphia
Philadelphia, Pennsylvania 19103

RICHARD D. ALEXANDER
Museum of Zoology, University of Michigan
Ann Arbor, Michigan 48109

WILLIAM CADE
Biological Sciences, Brock University
St. Catharines, Ontario L2S 3A1 Canada

ABSTRACT.—In New Caledonia the family Gryllidae is represented by 12 subfamilies, 28 genera and at least 87 species. In this work we describe nine new genera and 55 new species. The New Caledonian fauna, though close to Australia, is very distinctive and is represented by several species groups (*Notosciobia, Koghiella, Tremellia, Agnotecous, Adenopterus, Archenopterus, Calscirtus,* and *Matuanus*) which have radiated on the island. Much of this fauna seems to have radiated along the now mainly submarine Norfolk Ridge.[New Caledonia, crickets, Gryllidae, new species, songs, systematics, types]

HISTORY OF NEW CALEDONIA

The island of New Caledonia, centrally located among the submarine ridges, marginal basins, and island arcs of the South West Pacific forms a major link in the chain of islands running between New Guinea and New Zealand. It is situated on a submerged ridge which is part of the former tectonic block that detached from Austro-Antarctica between 78 and 56 million years ago. The block was split by the New Caledonia Basin, now located between Norfolk and Lord Howe islands, about 65 m.y. ago (Ballance 1980; Coleman 1980). This was a relatively shortlived plate which grew in surface through the formation of new sea floor along its western and southern margins (between Australia and Lord Howe Rise). It later fused to become a part of the active eastern margin of the much larger Australian plate which was moving in a northerly direction into the Pacific Plate, and was accompanied by the emergence of land along its eastern margins. The block now contains two marine ridges, united in the south in the vicinity of western New Zealand. The more eastern *Norfolk Ridge* runs from New Zealand to New Caledonia and includes Norfolk Island near its center. The western ridge, the *Lord Howe Rise*, runs from New Zealand in a NNW direction towards Queensland, but then at Lord Howe Island bends north to the Chesterfield Reefs. New Caledonia is part of the *Inner Melanesian Arc* (Carey 1938b; Glaessner 1950) which extends from the eastern most point of New Guinea through New Caledonia and

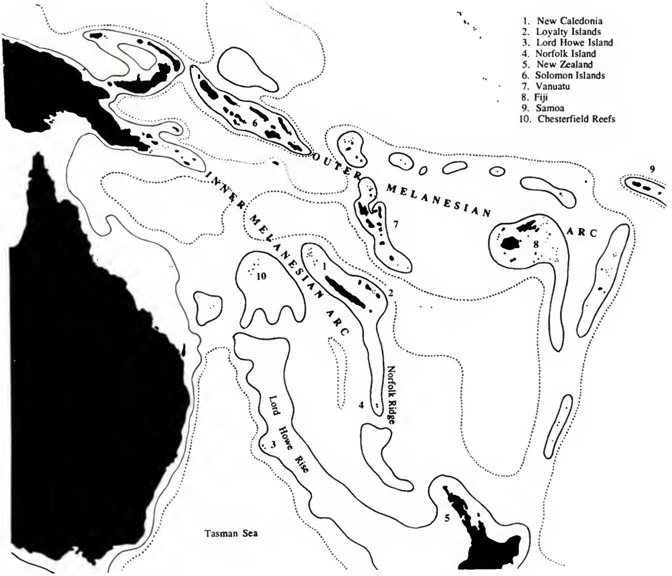


FIG. 1. Position of New Caledonia in the Southwest Pacific.

Norfolk Island to New Zealand. This arc is much older than another arc to the north which developed when a new front was established between Australian and Pacific plates; the newer *Outer Melanesian Arc* extends from northern New Guinea through New Britain, the Solomons, Vanuatu, Fiji, and Samoa, then southwards to the Kermadec Group.

Today New Caledonia is a French Territory in the southwest Pacific positioned at approximately 21S 166E; it lies about a thousand miles northeast of Brisbane, Australia, and a thousand miles NNE of New Zealand. Its nearest island neighbors are Vanuatu (the New Hebrides) 480 km NNE and the Loyalty Islands less than 150 km to the east. This narrow island (ca.390 km long and on averge 50 km wide) is much older than neighboring island groups. Its geological history relates more to northern New Zealand and southeast New Guinea. Its mountainous terrain, made up of ultramafic rocks, was produced through sea floor overthrust from the east sometime in the middle of the Tertiary. The three highest points are Mt Panié (1628m) in the north, Mé Maoya (1500m) in the center, and Mt Humboldt (1618m) in the south.

New Caledonia is one of the older land masses in Australasia. The first emergence of land in the area was probably in the upper Jurassic. Cretaceous deposits contain coal and suggest that alternation of land and marine facies took place until further episodes of uplift occurred in the Eocene, after which land in the area was probably always present in greater or lesser amounts. This would mean that land was in existence at the time of the dispersal of Gondwanaland from the beginning of the Cretacous onwards and could be reflected in the composition of the flora and fauna.

New Caledonia is noted for its old, diverse and highly endemic flora. It contains many presumed relicts from a Cretaceous Australasian-Antarctic flora which probably reached New Caledonia before the opening of the Tasman Sea. That sea subsequently isolated the island from the rainforest taxa flowing into Australasia from the Oriental tropics. The New Zealand flora may have arisen in a similar manner and was also shielded from competition from new invaders from the north.

More modern taxa did reach New Caledonia, some directly from Australia, possibly mainly during periodic exposures of the Chesterfield Reefs, but mostly through association with the Inner Melanesian Arc from New Guinea.

As Australia moved northwards, Indo-Malayan elements began to penetrate it in the early Tertiary, and this increased greatly in the closing stages of the Oligocene. Before and during the Miocene, access to Australasia was probably mainly from China via Taiwan, the Philippines, and the Outer Melanesian Arc, then to parts of the inner Arc and Australia.

Prior to the influx of Indo-Malayan elements a Melanesian biota had established itself all along the inner Melanesian Arc as shown by similarities between the vegetation of subtropical New Zealand, montane New Caledonia and highland New Guinea. As the land area increased in Indonesia in the Pliocene and Pleistocene, numerous more competitive but less dispersive Oriental plant taxa moved into Melanesia and displaced much of the Melanesian flora, particularly in New Guinea, though some elements were restricted to certain habitats such as high altitudes or poor soils. In such habitats the flora has held its own and has even advanced westwards into the Oriental Region.

CONNECTIONS TO AUSTRALIA

The more ancient southern elements in New Caledonia are most evident in the groups with poor powers of dispersal such as, among insects, the Ephemeroptera and Cerambycidae, but much less so in the more dispersive ones such as the Lepidoptera and to some extent the birds (Holloway 1977). These old connections are predominantly with Australia or with Australia and New Zealand together, particulary in the flora. There are few exclusive connections with New Zealand, except in some insect groups such as the Ephemeroptera, Trichoptera, and Cerambycidae. Phytogeographic patterns suggest that exclusive links between New Caledonia and New Zealand could have arisen through the extinction of Australian representatives during the increase of aridity and the consequent restriction of rainforests on the Australian continent throughout the later Tertiary. Such extinction would have been most likely in groups dependent on tropical rainforest conditions (Holloway 1977).

Colonization of New Caledonia from Australia may have occurred on several occasions through the Chesterfield Islands and almost certainly did during recent glaciations.

For highly disperisve groups of Lepidoptera the presence of these stepping stones was not essential, as indicated by the number of vagrant Australian species of Macroheterocera recorded on Norfolk over a period of six years (Holloway 1977).

A chain of islands on the Lord Howe Rise may have provided a route for interchange between New Caledonia and New Zealand.

The floristic and faunistic differences between New Caledonia and Fiji are large and Vanuatu, though much closer to New Caledonia, has a

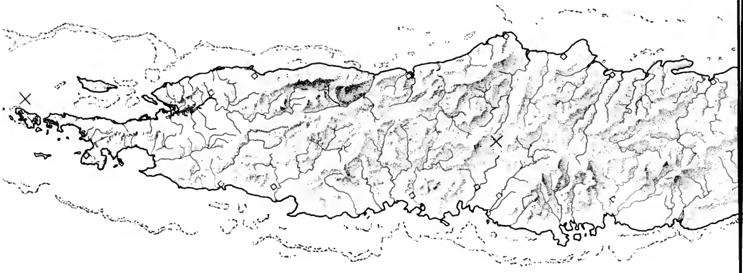


FIG. 2. New Caledonia, showing general relief.

biota which is much more closely related to that of Fiji.

ORIGIN OF CRICKET FAUNA

The crickets of New Caledonia can be divided into two elements: the endemic groups which are now restricted to the island and the recent dispersives which are widely distributed over the Southwest Pacific.

Widespread and highly dispersive groups which show no evidence of having speciated on New Caledonia may have been introduced relatively recently on the island. Some may have been carried there by man, but others are strong fliers and may have migrated there on their own. It seems more likely that they were introduced by humans, because they commonly inhabit areas tranformed by humans. Some may have been included in freight carried to the islands over the last 100 years or so, or their eggs could have been transported in soil or in plants imported there.

Brachytrupinae

New Caledonia has but one genus, *Notosciobia*, which is related to Australian *Cephalogryllus* and might even be considered congeneric with it. Whether it came directly from Australia or entered New Caledonia along the Inner Melanesian Arc cannot be determined until the New Guinea fauna is studied. We know only that superfically similar crickets occur in New Guinea and the western Solomons, but these have not been examined in detail. We have not found this group in Fiji, Samoa, Guadalcanal, or in the Caroline Islands.

Notosciobia shows a primary and secondary radiation; at least 15 species can be assigned to three species groups. Our sampling of the genus must be considered preliminary and it is likely that many more species will be found.

Gryllinae

The Gryllinae have enterned New Caledonia relatively recently. Only three species are known to occur there and all are widespread in the southwest Pacific and Australia. There is, as yet, no evidence of song and morphological differentiation there. By contrast the Gryllinae have penetrated much further along the Outer Melanesian Arc as far as Fiji.

Gryllini

The genus *Teleogryllus* ranges throughout sub-Saharan Africa, then eastwards through southern Asia to China and Japan, all of South-

east Asia, Australia, and the Pacific as far as Hawaii. The highest diversity is in Africa where at least three levels of radiation can be discerned. Only*Gryllus* in this subfamily has a wider distribution. Among other groups only *Gryllotalpa*, *Anaxipha*, *Pteronemobius* and *Oecanthus* have ranges of equivalent or greater size. Two species occur on New Caledonia. *T. oceanicus* occurs through much of the western Pacific and extends from Australia to Tahiti, and from the Caroline Islands to Hawaii. In the south it extends to Norfolk island. *T. marini* is known from eastern Australia, Fiji, and Samoa. The distribution of these two species in New Guinea and westwards is not yet known, but it is possible that they are widespread in Indomalaysia.

Modicogryllini

Lepidogryllus is the only member of this tribe in New Caledonia.The only species, *Lepidogryllus comparatus,* is also known from Australia and has reached as far east as Norfolk Island, New Caledonia, and the eastern Solomons. It is probably on New Guinea and Vanuatu as well. We did not find it in Fiji, Samoa, or the Caroline islands.

Nemobiinae

New Caledonia possesses two of three known tribes of Nemobiinae, namely the Nemobiini and Thetellini. The former is also known from Lord Howe Island, Norfolk Island, New Zealand, and Australia. The latter tribe is oceanic and ranges through much of the Indian and Pacific oceans. The radiation of the Nemobiini seems to be related to the breakup of the eastern edge of the Australian plate and the subsequent formation of the Inner Melanesian Arc.

Nemobiini

Bobilla is widespread over southeastern Australia and is also known from southwestern Australia, Tasmania, and New Zealand. In New Caledonia it is represented by two species, but additional species will probably be found. It does not occur on Lord Howe or Norfolk islands.

Koghiella is endemic to New Caledonia, but closely related to *Ignambina*, also from New Caledonia and *Dictyonemobius* from Lord Howe and Norfolk islands. The genus displays two levels of radiation in New Caledonia and is probably derived from the more widely distributed *Bobilla.*

Amonemobius. The placement of this species close to *Koghiella* is tentative, and is based principally on the close resemblance of the forewings to those of *Koghiella.*

Paniella and *Fikola.* The positions of these genera are uncertain, especially the latter, which is based on a single female. It may represent a wingless relative of *Koghiella*.

Thetellini

This tribe is presently known to extend from the east coast of Africa across to northern Australia and eastwards to Hawaii. It has not yet been collected near the American coasts, but may well extend across the entire Pacific. The members of this tribe are found along rocky and coral shorelines and are usually found in the splash zone. However, in Hawaii and on Krakatau they are also found on lava flows and in lava caves distant from the sea. Presently the tribe comprises the genera *Thetella, Apteronemobius, Caconemobius, Ionemobius* and perhaps *Orintia.* The last genus, recently described by Gorochov (1986) is, unfortunately, represented only by a single female.

Trigonidiinae

The Trigonidiinae have spread far and wide across the Pacific and are known from most islands. In some island systems they have speciated to an extreme degree and make up the bulk of the fauna (Hawaii, Fiji, and others). New Caledonia, however, presents a puzzle, for the subfamily is poorly represented there. We found only three species, two of which (*Trigonidomorpha sjöstedi* and *Metioche vittaticollis*) are widespread in Australia and the Pacific. The only other species, *Anaxipha caledonica*, though common on the island, appears to be the only endemic member of this subfamily. Why is such a highly dispersive group not better represented in New Caledonia? Did the group reach New Caledonia very late, or did it encounter well entrenched groups of crickets which had already usurped the normal trigonidiine niches? *Anaxipha caledonica* is now flightless and lives in the native forests, suggesting that it was not brought in by humans.

Pentacentrinae

This subfamily, though abundant in the region north of Australia, has not been found in New Caledonia or any other western or southwestern Pacific islands. This is surprising in view of the fact that many species are macropterus. Two species are known from Australia.

Phalangopsinae

This entirely flightless subfamily is very capable of crossing major bodies of water, though how it does so remains a mystery. It is represented in New Caledonia by a single genus, *Caltathra*, which seems most closely related to *Tathra* and *Endotaria* of Australia and *Nesitathra* of Norfolk Island. We do not yet know enough about the subfamily in New Guinea or in the Outer Melanesian Arc to say anything about how the group reached New Caledonia. The subfamily is also represented in the Southwest Pacific by *Howeta* and *Endacusta* on Lord Howe Island. Quite possibly these islands acquired these crickets early, during the breakup of the Australian plate. Though not generically diverse, the group is speciose in Australia. We have recently found the subfamily on Yap and Ponape in the Caroline islands. The subfamily has not been found on New Zealand, but may very well be found in the forests of North Island.

Itarinae

The origin of the only genus, *Tremellia*, is unknown and open to speculation. Australia itself has only one species and therefore seems an unlikely source. The presence of *Tremellia* in the Philippines and on Java suggests that it may have come to New Caledonia via New Guinea and the Inner Melanesian Arc. The subfamily, but not the genus, is present on Fiji but not Samoa. New Caledonia has five species of *Tremellia*, but it is likely that many additional species occur in the rain forests.

Euscirtinae

The members of this tribe are known from Africa to eastern Asia and Australia. The last continent contains five genera: *Euscyrtus*, *Merrinella*, *Turana*, *Tozeria*, and *Patiscus*. Little is known about this group north of Australia and it is not known to extend along the Outer Melanesian Arc. New Caledonia has only one genus and species (*Proturana subaptera*). It is quite similar to *Merrinella* in Australia. This group is not known in the eastern Solomon islands, Fiji, or the Caroline Islands.

Eneopterinae

Two genera of this world-wide group reached New Caledonia and one of them has radiated there. *Agnotecous*, seems most closely related to the Australian and Indomalasian genus *Lebinthus* and *Lebinthus*-like genera from the eastern Solomons and from the western Caroline islands. It seems likely that the genus came by way of the Inner Melanesian Arc and not directly from Australia where *Lebinthus* is represented by only two species. *Lebinthus*-like eneopterines are absent from Fiji and Samoa.

The other genus, *Cardiodactylus*, is widespread through the western Pacific. It is especially prevalent in New Guinea and along the Outer Melanesian Arc, to Fiji and Samoa, and is also present in New Guinea and the western Caroline Islands. We found a single species in New Caledonia. One species is known from Austalia. The genus evidently does not extend beyond New Caledonia.

Podoscirtinae

This subfamily is represented in New Caledonia by five genera; three of them are endemic, another is shared with Norfolk island; and only *Aphonoides* extends outside of the Inner Melanesian Arc.

Aphonoides. is widespread in Australia and New Guinea. It has not yet been seen in New Caledonia, but since one species has been collected in the Loyalty Islands, it is likely to occur on New Caledonia as well.

Calscirtus and *Insulascirtus*. This clade radiated in the central Inner Melanesian Arc. Superficially it is similar to *Tamborina* and *Madasumma* of Australia, though the genitalia and the body shape suggest that it is not derived from either. *Calscirtus* is confined to New Caledonia and is represented by three species, though many more species probably exist in the rain forests. It is most closely related to *Insulascirtus*, a genus of wingless species from Lord Howe Island (five species) and Norfolk Island (two species).

Adenopterus and Archenopterus. *Adenopterus* was previously known only from Norfolk Island, though one species, previously under *Munda*, had been described from New Caledonia. The present distribution of the genus is New Caledonia (15 species), Loyalty Islands (one species), and Norfolk Island (one species). It is related and probably derived from the new genus *Archenopterus* which is known only from New Caledonia (six species). These genera are not closely similar to any Australian genera, and have several very odd morphological characteristics not seen anywhere else in the world. This group, like *Calscirtus* and *Insulascirtus*, radiated in the central Inner Melanesian Arc.

Oecanthinae

Aside from a single introduced, or, perhaps, recent immigrant (*Oecanthus rufescens*), tree crickets are absent from New Caledonia. This state of affairs is reminiscent of Trigonidiinae. *O. rufescens* is widespread in Australia and also known from the eastern Solomons and Fiji. Tree crickets are also absent from Fiji (except for the above-noted *O. rufescens*) and from Samoa; nor have they reached the Caroline Islands (Palau, Yap, Ponape). Two genera have speciated in Australia and New Guinea, so it is surprising that the subfamily has not reached New Caledonia or Fiji. It is especially surprising since the Oecanthines have undergone three to four levels of radiation in Hawaii. The absence of the subfamily in the southwest Pacific suggests perhaps that tree crickets reached Hawaii from the Americas.

Pteroplistinae

This subfamily extends from India to Fiji and into the western Caroline islands (Palau). It has not yet been found along the Inner Melanesian Arc.

Mogoplistinae

Scaly crickets are well represented in New Caledonia. The taxonomy of this group is very difficult and we have not included them in this work. Several species appear to resemble species from the mangroves in Queensland. Mogoplistines have penentrated most of the Pacific islands inspite of the fact that no members fly. Probably their eggs are deposited in wood and are carried from island to island.

Gryllotalpinae

We did not encounter mole crickets in spite of the fact that we often listened for them in places which seemed suitable. Chopard (1915), however, lists *Gryllotalpa australis* (Erichson) from the Loyalty Islands. The subfamily seems to be largely absent from the southwest Pacific islands (New Caledonia, Fiji, Samoa), which is surprising since it has penetrated the Caroline Islands as far as Ponape. New Zealand has the genus *Triamescaptor*.

Myrmecophilinae

Although this group is world-wide in distribution it is not known from in New Caledonia. However, we made no concerted effort to find it and believe that it will eventually be found in ant nests.

MUSEUM DEPOSITORIES

ANN ARBOR: University of Michigan Museum of Zoology
BASEL: Naturhistorishes Museum
BUDAPEST: Zoological Department, Hungarian Natural History Museum
HONOLULU: Bernice P. Bishop Museum, Honolulu
LENINGRAD: Zoological Institute, Academy of Sciences, USSR
PHILADELPHIA: Academy of Natural Sciences of Philadelphia
VIENNA: Naturhistorishes Museum

MORPHOLOGICAL ABBREVIATIONS

M	male
MN	male nymph
F	female
FN	female nymph
RW	rostral width (measured at anterior ex tremity)
SW	scape width (width of basal antennal segment)
PL	pronotal length (measured along the midline)
PW	pronotal width (greatest width)
FWL	forewing length (greatest length from posterior margin of pronotum
ML	mirror length (greatest overall longitu dinal length)
MW	mirror width (greatest overall horizon tal length)
FL	hind femur length
FW	hind femur width (greatest width)
TL	tibial length (not including apical spurs)
CL	cercal length
OL	ovipositor length (measured from upper base of ovipositor to tip)
SPS	spermatophore sac.
MAPs	muscle attachment plate (two drop-shaped markings in anterior half of pronotal disk.
p/s	pulses per second
ch/s	chirps per second
chL	chirp length
KHz	frequency in kiloherz
°C	degrees centigrade

COLLECTING SITES

3. Ducos Penisula, near Noumea, dry brushy roadside, 26 ii 1983.
4. Yahoue, near Noumea, forest and stream, 27 ii 1983.
5. Mount Koghi, west slope of Mount Bouo, tall rainforest, 27 11 1983.
6. East coast, about 12 km southeast of Thio,

forest along beach, 28 ii1983.

7. Negropo, near Canala, disturbed forest, 1 iii 1983.
8. 14 km west of Canala, 1 iii 1983.
10. 25 km west of Canala, road through forest, 1 iii 1983.
11. 27 km west of Canala, road through forest, 1 iii 1983.
12. 28 km west of Canala, road through forest, 1 iii 1983.
13. 34 km west of Canala, road through forest, 1 iii 1983.
14. Poe Beach, West of Borail, beach area, 1 iii 1983.
15. 43 km west of Houaïlou, forest, 2 iii 1983.
16. 40 km west of Houaïlou, forest, 2 iii 1983.
17. Tenemba River Valley, east of Tenemba, near Ponérihouen, 3 iii 1983.
18. Tiéte, north side of Poindimié, beach, 3 iii 1983.
19. Amoa River Valley, near Poindimié, grassy roadside, 3 iii 1983.
20. Amoa River Valley, 3 km west of main road, near Poindimié, 3 iii 1983.
21. Amoa River Valley, 6.4 km west of main road, near Poindimié, forest, 3 iii 1983.
22. Amoa River Valley, 8.4 km west of main road, near Poindimié, forest, 3 iii 1983.
23. Tiwaka River Valley, 5 km west of main road, near Poindimié, 3 iii 1983.
24. Hienghene, grottoes south of town, near beach, 5 iii 1983.
25. Hienghene, ca. 4 km west of bridge, 5 iii 1983.
26. about 10 km southeast of Oubatche, coastal forest, 6 iii 1983.
27. about 17 km southeast of Oubatche, coastal forest, 6 iii 1983.
28. about 14.9 km southeast of Oubatche, coastal forest, 6 iii 1983.
29. Koumac, grottoes area, 7 km east of town, 7 iii 1983.
30. mountain forest above Koné, road to Panaki, 7 iii 1983.
31. beach west of Koné, Plage de Foe, 8 iii 1983.
32. near Nétlial, 8 iii 1983.
33. stream near Goipin, northwest of Nékiaï and Poya, stream and forest, 8 iii 1983.

List of Species

Brachytrupinae
  Cephalogryllini
    Notosciobia Chopard
    Nola Group
      nola Otte, n. sp.
      goipina Otte, n. sp.
      canala Otte, n. sp.
      paranola Otte, Otte, n. sp.
      thiensis Otte, n. sp.
      animata Otte, n. sp.
      puebensis Otte, n. sp.
      oubatchia Otte, n. sp.
      rouxi Chopard
      velutina Chopard
      lifouensis Gorochov 1986 (from *Cephalogryllus*)
    Poya Group
      poya Otte, n. sp.
    Fausta Group
      fausta Otte, n. sp.
      rex Otte, n. sp.
      hirsuta Otte, n. sp.
    Tape recorded species
      [konensis] song species
      [parapoya] song species

Gryllinae
  Gryllini
    Teleogryllus
      oceanicus (Le Guillou)
      marini Otte & Alexander

  Modicogryllini
    Lepidogryllus Otte and Alexander
      comparatus (Walker)
    Gryllus lepidoides Chopard 1915: 138.
      Synonym of *Lepidogryllus comparatus* Walker

Nemobiinae
  Nemobiini
    Bobilla Otte & Alexander
      avita Otte, n. sp.
      pacifica Gorochov 1986 (from *Bullita*)

- **Koghiella** Otte, n. gen.
  - **bouo** Otte, n. sp.
  - **parabouo** Otte, n. sp.
  - **semibouo** Otte, n. sp.
  - **thio** Otte, n. sp.
  - **caledonica** Chopard 1970 (from *Dictyonemobius*)
- **Ignambina** Otte, n. gen.
  - **oubatchia** Otte, n. sp.
- **Amonemobius** Otte, n. gen.
  - **vexans** Otte, n. sp.
- **Paniella** Otte, n. gen.
  - **apterus** (Chopard) (from *Nemobius* (*Pronemobius*))
- **Apteronemobius** Chopard
- *Paora* Gorochov 1986 (new synonym)
  - **gusevae** Gorochov 1986

Thetellini

- **Ionemobius** Otte, n. gen.
  - **alliciens** Otte, n. sp
- **Fikola** Gorochov 1986
  - **fusca** Gorochov 1986
- **Orintia** Gorochov 1986
  - **incrustata** Gorochov 1986

Trigonidiinae

- **Trigonidomorpha** Chopard
  - **sjöstedti** Chopard
- **Metioche**
  - **vittaticollis** Stal
  - **flavipes** Saussure
- **Anaxipha** Saussure
  - **caledonica** Otte, n. sp.

Phalangopsinae

- **Caltathra** Otte, n. gen.
  - **dubia** Chopard (from *Endacustes*)
    - *steinmanni* Gorochov 1986
  - **panaki** Otte, n. sp.

Itarinae

- **Tremellia** Stal
  - **sarasini** (Chopard 1915)
  - **caledonica** Otte, n. sp.
  - **alpha** Otte, n. sp.
  - **beta** Otte, n. sp.
  - **tiwaka** Otte, n. sp.

Eneopterinae

- **Agnotecous** Saussure
  - **obscurus** Chopard 1970 (from *Lebinthus*)
  - **yahoue** Otte, n. sp.
  - **tapinopus** Saussure 1978
  - **brachypterus** Gorochov 1986
  - **novaecaledoniae** Gorochov 1986
  - **robusta** (Chopard 1915) (from *Eurepa*)
- **Cardiodactylus** Saussure
  - **novae-guineae** (de Haan)

Euscyrtinae

- **Proturana** Otte, n. gen.
  - **subaptera** (Chopard 1970) from *Euscyrtus*

Podoscirtinae

- **Adenopterus** Chopard
- *Peltia* Gorochov 1986 (new synonym)
- *Kraussi Group*
  - **kraussi** Otte, n. sp.
  - **sylvaticus** Otte, n. sp.
  - **sarasini** Chopard (from *Munda*)
  - **rouxi** Chopard (from *Munda*)
  - **roseola** Gorochov 1986 (from *Peltia*)
  - **caledonicus** Otte, n. sp.
  - **dumbeus** Otte, n. sp.
  - **confixus** Otte, n. sp.
  - **dubius** Otte, n. sp.
  - **perplexus** Otte, n. sp.
  - **paraperplexus** Otte, n. sp.
  - **euperplexus** Otte, n. sp.
- *Sarrameus Group*
  - **sarrameus** Otte, n. sp.
  - **yahouensis** Otte, n. sp.
  - **tchambicus** Otte, n. sp.
  - **admirandus** Otte, n. sp.
- Crouensis Group
  - **crouensis** Otte, n. sp.
  - **lifouensis** Otte, n. sp.
  - **saussurei** (Chopard)(from *Munda*)
  - **baloghi** Gorochov 1986
- **Archenopterus** Otte, n. gen.
  - **gressitti** Otte, n. sp.
  - **maai** Otte, n. sp.
  - **hemipteroides** Otte, n. sp.

- **bouensis** Otte, n. sp.
- **amoensis** Otte, n. sp.
- **hemiphonus** Otte, n. sp.

Aphonoides Chopard
- **ouveus** Otte, n. sp.

Calscirtus n. gen.
- **amoa** Otte, n. sp.
- **paniensis** Otte, n. sp.
- **timbiensis** Otte, n. sp.

Matuanus Gorochov 1986
- **priapus** (Saussure)(from *Munda*)
- **elegans** Otte, n. sp.
- **caledonicus** (Saussure) (from *Aphonoides*)
- **flavomaculatus** Gorochov 1986
- **neoplumus** Otte, n. sp.
- **rufidulus** (Saussure)(from *Munda*)

Oecanthinae
- **Oecanthus rufescens** Serville

Gryllotalpinae
- **Gryllotalpa australis** (Erichson)

Nomina Dubia
- Podoscirtinae
  - **Tapinopus platyceps** Saussure (type lost?, replacement specimen is from southern Africa)

Other species listed from New Caledonia

Munda insularis Saussure 1878: 639. This species is listed from Fiji and New Caledonia (the latter specimen from the Vienna museum was called a variety belongs to *Adenopterus crouensis* n.sp.)

Munda tacita (Saussure). The species was described from "New Guinea ?" Chopard 1967 lists it from New Caledonia, but it is very doubtful that it occurs there.

Teleogryllus commodus Walker listed from New Caledonia is probably *T. oceanicus* or *T. marini*.

BRACHYTRUPINAE

Cephalogryllini

NOTOSCIOBIA Chopard

Notosciobia Chopard 1915: 140. Type species: *N. rouxi* Chopard (New Caledonia).

RECOGNITION OF GENUS. Male epiphallus bilobed, separated by a wide U-shaped gap; lobes terminating in points; spermatophore tube mold long or short; ectoparameres variable in shape; virga usually very long and slender, short in slender in the Poya Group. Pronotum longer than wide, with a distinct groove in the posterior half of each lateral lobe; with roughly parallel sides or front of pronotum wider than posterior. Forewings with an incomplete mirror (or a mirror with poorly defined posterior margin and mostly filled with cells)(usually with well defined posterior margin and not divided into cells in Australian *Cephalogryllus*. Hind tibiae short. Pronotum and legs very pubescent. Without hindwings. Dorsum of abdomen with a row of small narrow dark horizontal lines running laterally on each tergite. Legs usually very light brown, tibiae slightly darker and with a dark brown on lower face. Tympana present only on outer face. Without a median ocellus, although in some species the location of the ocellus is still evident. Occiput, entire pronotum, legs and abdomen covered with short fine pubescence. Hindwings absent. Fore- and middle tibiae with 3 and 4 apical spurs respectively.

BIOLOGY. All species in this genus have been found in leaf litter on the forest floor and all were found in wet forest on the crest of the mountain or in moist ravines. They were found at sea level only on the windward side of the island. Some of the species live in burrows in the juvenile stages and adults of several species were also associated with burrows where they were found with nymphs of all stages. Several species were found under rotting logs. The songs are all relatively simple and are often given in bursts, such that long silent periods alternate with periods when a number of males sing simultaneously. In some species males that sing near one another alternate in the production of songs.

Nola Group

Distinguished from the Poya Group by the shape of the epiphallic lobes and the large size of the spermatophore tube mold.

Notosciobia nola Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Yahoué, near Noumea, forest floor, 27 ii 1983 (Alexander, Cade & Otte #4). ANN ARBOR.

RECOGNITION. Figs.4, 6A, 7. Tables 1, 2. Song consisting of short trains of rapidly delivered pairs of pulses. Harp with three veins. Unlike *paranola* each ectoparamere is distinctly bilobed at the apex, epiphallus with a more V-shaped gap, file with fewer than 100 teeth. Ectoparameres most similar to *goipina*, but differs in song and in having fewer than 100 teeth. Differs from *canala* in having excised ectoparameres and in the male song.

Males: Large for genus. Head and pronotum dark brown to black. Wings and abdomen greyish-brown. Head: dorsum dark brown to black; face and cheeks dark brown. Pronotum: dorsum dark brown to black, MAPs reddish. Forewings: dark brown to black in basal and apical areas and lateral field. Hindfemora with brown oblique stripes on outer face; region just before knees dark brown; tibiae mostly dark brown.

SONG. Short trains of rapidly delivered pairs of pulses (Fig. 4).

HABITAT. Several males were heard singing on a steep forested bank. We caught one of them that was hidden beneath rotting logs.

SPECIMENS. *Holotype* M, ANN ARBOR.

Notosciobia goipina Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, 40 km west of Houaïlou, rain forest, 2 iii 1983 (Alexander, Cade & Otte). ANN ARBOR.

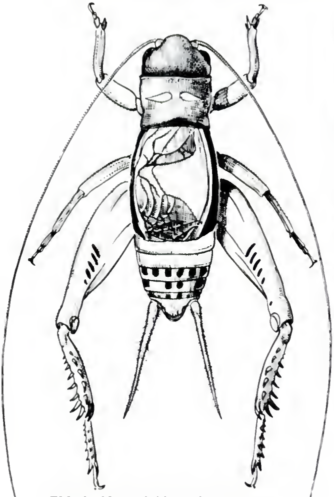


FIG. 3. *Notosciobia animata* male.

RECOGNITION. Figs. 4, 6B, 8. Tables 1, 2. Most similar to *nola* (genitalia largely indistinguishable) but file with more than 100 teeth, and song with higher pulse and chirp rates.

Males: Large for genus. Head and pronotum dark brown to black. Pronotum: dorsum wider in anterior than posterior end, dark reddish brown, MAPs reddish brown; lateral lobes dark reddish brown to black. Forewings: dorsum dark brown to black in basal and apical areas and on lateral field. Abdomen: spotted and blotchy with gray and dark brown; venter pale, subgenital plate brown. Legs all pale. Hindfemora with rows of small brown markings.

HABITAT. Collected in forest on a bank above a small creek where it was found in leaf litter.

SONG. Short groups of double-pulse chirps.

SPECIMENS. *Holotype* M, ANN ARBOR. *Paratypes:* (PHILADELPHIA and ANN ARBOR) Same data as holotype, 2M. Near Goipin, northwest of

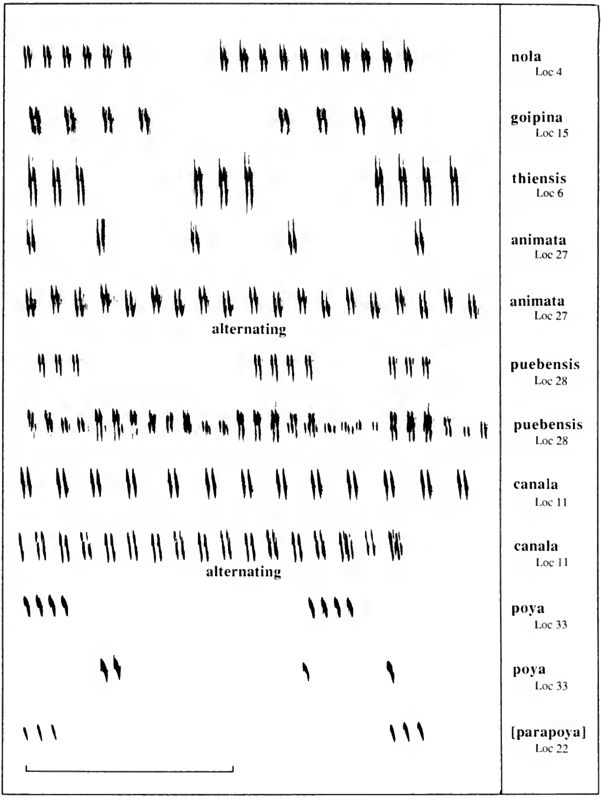


FIG. 4. *Notosciobia* songs in the Nola and Poya groups. For *animata* and *canala* the songs of soloing and alternating males are shown (Loc, locality where recording was made).

Table 1. Comparison of Notosciobia species. (For abbreviations see Methods).

	No. file teeth	BL	FL	CL	FWL/PL	TL/FL	Subapical spurs in./out.
nola							
HM	97	23	13.5	11	1.92	0.54	6/6
goipina							
HM	109	25	14	9.5	1.98	0.54	6/6
PM Loc16	109	23	12.9	-	-	-	-
PM Loc 33	102	27	14	7.7	1.75	0.57	6/6
thiensis							
HM	123	19	11.2	7.5	2.7	0.58	6/5
PF		21	10.5				6/5
PF		19	11				6/6
paranola							
HM	111	24	15	9.5	2.5	-	6/6
animata							
HM	103	15	9	5.4	2.36	0.56	6/5
PM	103	14	8.5	5.2	2.4		6/6
PM	110	14.8	8.7			0.55	7/6
PM	108	14.5	9	5.7	2.36		6/6
PF		15	8.5	5.9			5/6
oubatchia							
HM	79	14	9.3	6.8	2.1	0.51	4,5/5,6
canala							
HM	96	24	13.5	8.3	1.89	0.53	6/7
puebensis							
HM	98	17	9.8	6	2.4	0.54	6/5
rouxi							
HM	100	24	15	11	1.43	0.59	6/5
velutina							
HM	67	17	12	7.2	1.4	0.41	5/6
poya							
HM	ca. 140	14.5	9	5.7	3.09	-	5,5/3,4
fausta							
HM	88	14.5	8.4	5.6	1.75	0.57	4/3
rex							
HM	65	16	9.6	-	1.71	-	5/5
hirsuta							
HM	70	14	8	5	2.14	-	5/4

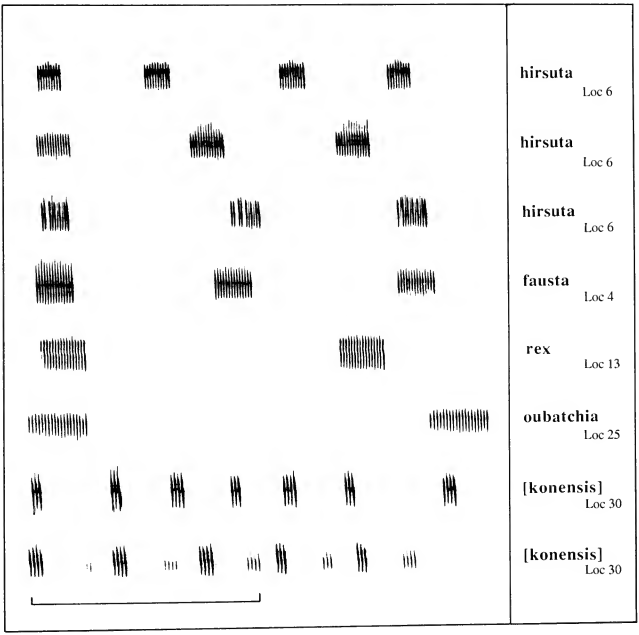


FIG. 5. *Notosciobia* songs in the Fausta Group.

Nékiaï and Poya, 8 iii 1983 (Alexander, Cade & Otte #) 1M.

Notosciobia canala Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, ca. 28 km w of Canala, 1 iii 1983 (Alexander, Cade & Otte). PHILADELPHIA.

RECOGNITION. Figs. 4, 6K, 9. Table 1, 2. Most similar to *goipina* and *nola*, but ectoparameres without a ventral depression at apex, and song consisting of a continuous train of double-pulse chirps.

Male: Head: dorsum dark reddish brown; face dark reddish brown. Pronotum: dorsum slightely lighter than head, with red MAPs. Forewings: ligher brown in central area dark brown in basal and apical areas and on lateral field. Abdomen: mostly light brown but each tergite with transverse row of small dark streaks. Fore- and midfemora pale brown and with dark brown along the lower distal surfaces. Hindfemora pale brown with dark brown oblique stripes on outer face.

SONG. A rapid train of double pulse chirps. Males singing near one another may alternate their chirps.

HABITAT. Rain forest, and along the steep vegetated road banks at the forest margin.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratype*: same data as holotype, 1M, ANN ARBOR.

Notosciobia paranola Otte, n. sp.

TYPE. *Holotype M*. New Caledonia, Mt. Koghi, west slope of Mt Bouo, tall forest, 27 ii 1983 (Alexander, Cade & Otte). PHILADELPHIA.

RECOGNITION. Figs. 6I, 7. Tables 1, 2. Differs from the similarly sized *nola* in having a forewing which is more than twice the length of the pronotum (see also *nola* recognition) and in the shape of the ectoparameres. Similar to *thiensis* in male genitalia but considerably larger and with 5 harp veins.

Male: Head dark brown; pronotum rusty brown; abdomen spotted pale and brown on dorsum. Forewings more that twice the length of the pronotum. Hindfemora with faint brown stripes on outer face.

SONG. Not known.

HABITAT. Found along a trail in a tall montane forest.

SPECIMENS. *Holotype* M, PHILADELPHIA.

Notosciobia thiensis Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, ca. 12 km south of Thio, in forest along beach, 28 ii 1983 (Alexander, Cade & Otte). PHILADELPHIA.

RECOGNITION. Figs. 4, 6C, 7. Tables 1, 2. Morphologically very similar to paranola but harp with only three veins, file with over 120 teeth, body length less than 20 mm, Hindfemora length less than 12 mm.

Male: Light reddish brown head and pronotum and yellowish legs. Head: dorsum reddish brown with 6 very faint pale stripes on occiput and vertex; face and cheeks reddish brown. Pronotum uniformly reddish brown. Forewings pale grey brown, becoming much darker in basal and apical areas and on lateral field. Abdomen pale brown. Legs ivory colored. Hindfemora with light brown oblique streaks on outer and inner faces, and with a pale streak along the upper crest, with dark red brown marks on inner and outer faces just before the knees. Hindtibiae pale brown on upper face, dark on lower face.

Females: coloration similar to male; forewings very small and non-overlapping, appearing as small hemicircular pads at posterior margin of pronotum. Ovipositor about half as long as pronotum.

SONG. Short bursts of double-pulse chirps.

HABITAT. Collected in leaf litter among rotten branches in a forest along the beach.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratypes*: same data as holotype, 2M, 2F, ANN ARBOR & PHILADELPHIA.

Notosciobia animata Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, 17 km southeast of Oubatche, coastal forest, 6 iii 1983 (Alexander, Cade & Otte #27). PHILADELPHIA.

RECOGNITION. Figs. 4, 6D, 8. Tables 1, 2. Song consisting of trains of double-pulse chirps. Spermatophore sac relatively short (in *oubatchia* it is also short, but the ectoparameres are bilobed at the apex).

Males: Head and pronotum reddish; forewings greyish; abdomen light brown. Head: dorsum reddish; face and cheeks reddish. Prontum uniformly reddish. Forewings greyish. Abdomen light brown. Legs all yellowish brown. Hindfemora without distinct outer oblique stripes.

Female: same color and size as male; ovipositor about one third as long as pronotum.

SONG. Trains of double-pulse chirps. Adjacent males may alternate with one another in the production of double-pulse units (Fig. 4). This

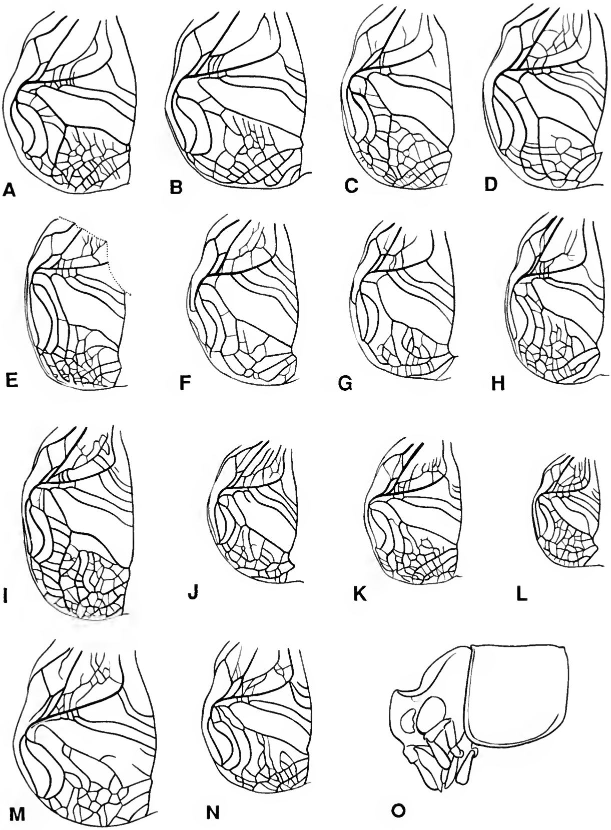


FIG. 6. *Notosciobia*. A-N, forewings (all but *goipina* of holotype). A, *nola*. B, *goipina* paratype. C, *thiensis*. D, *animata*. E, *poya*. F, *fausta*. G, *hirsuta*. H, *oubatchia*. I, *paranola*. J, *rex*. K, *canala*. L, *puebensis*. M, *rouxi*. N, *velutina*. O, *rouxi* head and pronotum of holotype.

behavior is very similar to that of *canala*.

HABITAT. Leaf litter in a dense coastal forest. The species lives in burrows.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratypes*: same data as holotype, 13M, 1F, PHILADELPHIA & ANN ARBOR.

Notosciobia puebensis Otte, n. sp.

TYPE. *Holotype M*. New Caledonia, 14.8 km southeast of Oubatche, coastal forest, 6 iii 1983 (Alexander, Cade & Otte). ANN ARBOR.

RECOGNTION. Figs. 4, 6L, 8. Tables 1, 2. Song consists of short burst of double-pulse chirps similar to *thiensis*. Harp with 6 veins; last harp vein connected to mirror in holotype. Genitalia similar to *animata*, but spermatophore sac much longer. Hindfemora without oblique dark stripes on outer face.

Male: Head, pronotum and forewings reddish brown. Abdomen: pale brown. Legs all pale brown. Hindfemora without dark oblique stripes on outer face.

SONG. Short groups of double pulse chirps.

HABITAT. Found in leaf litter in coastal forests.

SPECIMENS. *Holotype* M, ANN ARBOR.

Notosciobia oubatchia Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Hiengene, 4 km W of Bridge (Alexander, Cade & Otte) ANN ARBOR.

RECOGNITION. Figs. 5, 6, 9. Tables 1, 2. Male genitalia similar to *animata*, but ectoparameres bilobed at apex; song consisting of short chirps with a very rapid pulse rate.

Male: Head: dark reddish brown on dorsum and face; cheeks reddish brown. Pronotum: dorsum dark brown; lateral lobes dark brown, but lighter along anterior and lower margin. Forewings: reddish brown, but becoming black in apical area. Abdomen: dorsum dark brown, but each tergite with four pale spots. Fore- and midlegs: ivory colored. Hindfemora pale but with oblique dark brown stripes on outer face.

SONG. Widely spaced short chirps with a rapid pulse rate.

HABITAT. Rainforest on the northeast side of New Caledonia.

SPECIMENS. *Holotype* M, ANN ARBOR.

Notosciobia rouxi Chopard

Notosciobia rouxi Chopard 1915: 141. *Holotype M*, New Caledonia, Mont Ignambi, alt. 800 m, 8 viii 1911. BASEL.

RECOGNITION. Figs. 6M,O, 10. Table 1. Head of male with a huge concavity on the forehead. Ectoparameres distinctly notched at apex. Forewing with no traces of a mirror.

SPECIMENS. *Holotype* M, BASEL.

Notosciobia velutina Chopard

Notosciobia velutina Chopard 1915: 144. 2 males types, NewCaledonia, Foret du Mont Panié, alt. 500 m, 27 vi 1911. BASEL.

RECOGNITION. Figs. 6N, 10. Table 1. Distinguished from other members of this group in the configuration of the male genitalia.

SPECIMENS. *Holotype* M, BASEL.

Notosciobia lifouensis Gorochov, n. comb.

Cephalogryllus lifouensis Gorochov 1986:704. *Holotype M*, Lifou Island, Loyalty Islands. LENINGRAD. NEW COMBINATION. Type not examined.

RECOGNITION. See Figs 76-79 in Gorochov 1986:707. Gorochov mistakenly placed this species in *Cephalogryllus*. Examination of his figures shows a striking resemblance of this species to *Notosciobia* (Nola group) of New Caledonia.

Poya Group

Distinguished from the Nola and Fausta Group in having a deep median gap in the epiphallus and in

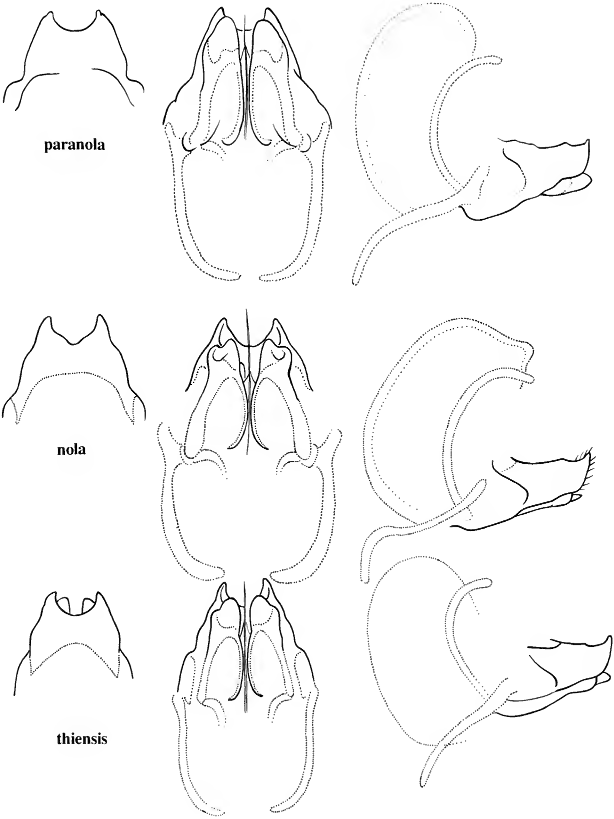


FIG. 7. *Notosciobia* (Nola group) male genitalia (holotypes).

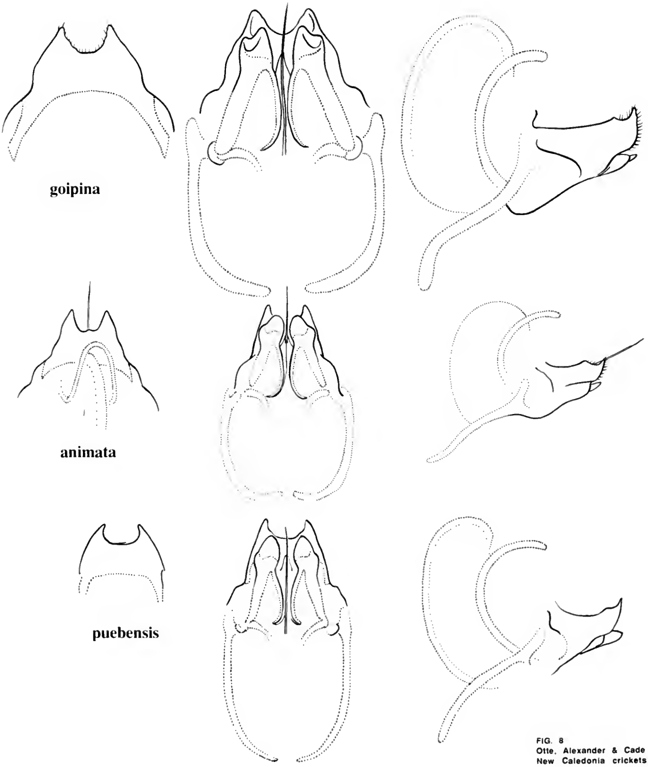


FIG. 8. *Notosciobia* (Nola group) male genitalia (holotypes).

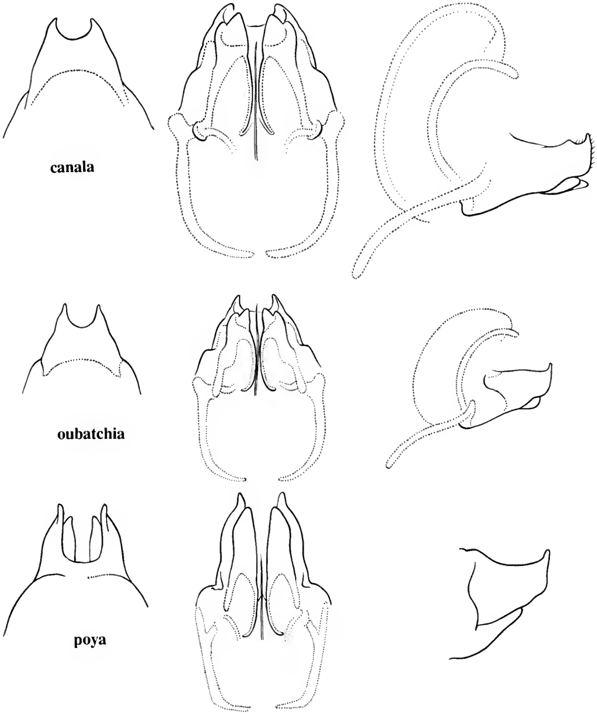


FIG. 9. *Notosciobia* (Nola and Poya groups) male genitalia (holotypes).

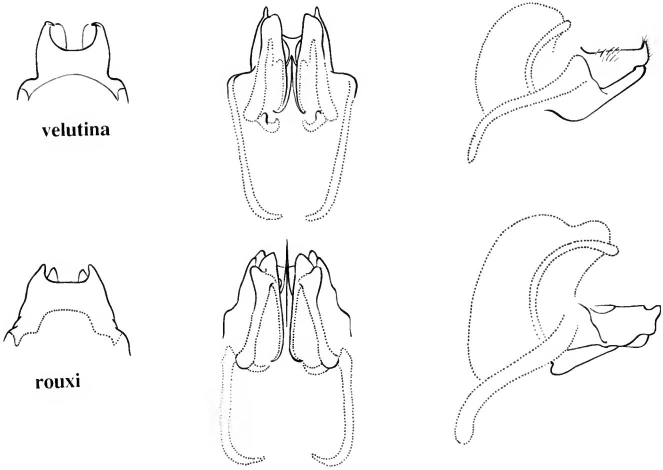


FIG. 10. *Notosciobia* (Nola group) male genitalia (holotypes).

having very long ectoparameres. Like the Fausta group it has a very short spermatophore sac.

Notosciobia poya Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, near Goipin, northwest of Nékiaï, forest along stream, 8 iii 1983 (Alexander, Cade & Otte #33). PHILADELPHIA.

RECOGNITION. Figs. 4, 6E, 9. Tables 1, 2. Male epiphallus with a deep U-shaped median gap; ectoparameres very long. Song consists of chirps with one to four pulses.

Male: Body color reddish brown. Head: dorsum with five broad black bands separated by narrow reddish bands; face and cheeks brown. Pronotum: dorsum brown, posterior margin black; lateral lobes brown. Forewings: dorsum brown, apical area no darker than central area. Legs: femora pale yellow-brown; tibiae slightly darker especially on lower face. Hindfemora with brown oblique stripes.

SONG. Chirps containing from one to four pulses.

HABITAT. Forest floor litter, on a bank above a small creek. Males live in burrows.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratype:* same data as holotype, 1M, ANN ARBOR.

Fausta Group

Distinguished from the Nola and Poya groups in having a distinctly V-shaped central cleft in the epiphallus, in having a very short spermatophore sac and in having inward turning ectoparameres.

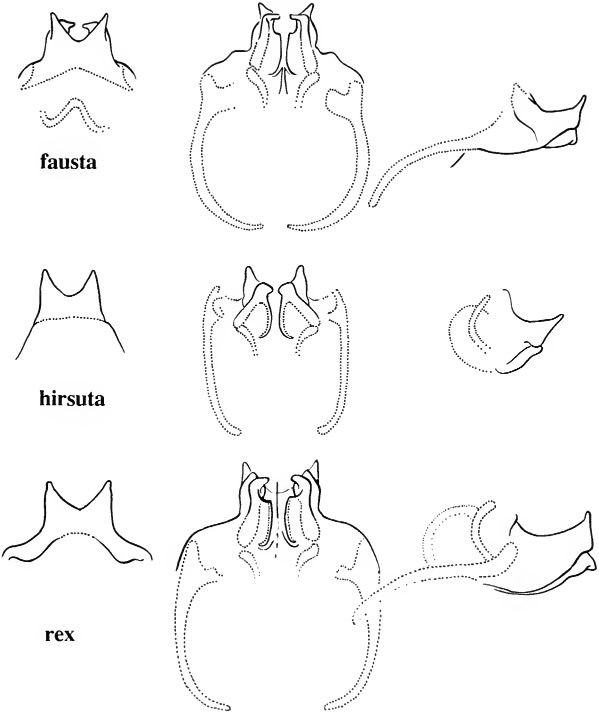


FIG. 11. *Notosciobia* (Fausta group) male genitalia.

Notosciobia fausta Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Yahoué, near Noumea, forest floor, 17 ii 1983 (Alexander, Cade & Otte # 4). PHILADELPHIA.

RECOGNITION. Figs. 5, 6F, 10. Tables 1, 2. Ectoparameres narrow and turned sharply inwards at apex. Epiphallus distinctly longer than in *hirsuta*. Song very similar to *hirsuta* and *rex.*

Male: Head reddish, pronotum reddish and black; abdomen speckled. Head: entirely reddish. Pronotum: dorsum dark reddish brown, posterior third black; lateral lobes dark reddish brown, but becoming ivory colored in lower front corner. Forewings: dorsum brown, darker in apical area; lateral field dark brown. Abdomen: dorsum mottled, venter uniformly pale. All femora ivory colored. Hindfemora with brown oblique stripes on outer face.

SONG. A succession of short chirps with a very rapid pulse rate.

HABITAT. Forest floor among litter in a tall forest above a small stream.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratype:* same data as holotype, 1M, ANN ARBOR.

Notosciobia rex Otte, n. sp.

TYPE. *Holotype M*. New Caledonia, 34 km west of Canala, 1 iii 1983 (Alexander, Cade & Otte). PHILADELPHIA.

RECOGNITION. Figs. 5, 6J, 11. Tables 1, 2. Male quite similar to *fausta* epiphallus not so slender at apex (side view) and apex of ectoparameres not turning in so sharply.

Male: Very similar to *hirsuta*, but differing in the shape of the ectoparameres.

SONG. A succession of short chirps with a very rapid pulse rate.

HABITAT. Rain forest along mountain road.

SPECIMENS. *Holotype* M, PHILADELPHIA.

Notosciobia hirsuta Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, about 12 km south of Thio, forest along beach, 18 ii 1983 (Alexander, Cade & Otte #6). PHILADELPHIA

RECOGNITION. Figs. 5, 6G, 11. Tables 1, 2. Ectoparameres rounded at apex and without an angular projection along inner margin (as in *rex* and *fausta*). Song similar to *fausta*, but sometimes pulses produced in pairs.

Male: Head and pronotum dark reddish brown. Pronotum: dorsum dark reddish brown, anterior margin and posterior third black, MAPs orange; lateral lobes dark reddish brown in anterior two-thirds and blackish in posterior third. Forewings: dorsum brown to dark brown in apical area; lateral field dark brown. Legs all pale yellowish brown. Hindfemora with faint oblique stripes, brown before knees on inner, outer and upper faces.

SONG. A train of short chirps with very rapid pulse rates.

HABITAT. Leaf litter and debris on forest floor along a beach.

SPECIMENS. *Holotype* M, PHILADELPHIA.

TAPE RECORDED SPECIES

[Notosciobia konensis]

This species was tape recorded at Loc 30. It inhabited forest litter. The structure of its song shows that it belongs to the Nola group (Fig. 5).

[Notosciobia parapoya]

This species was tape recorded in a forest at Loc 22. Its song suggests that it belongs to the Poya group.

Subfamily GRYLLINAE
GRYLLINI

Teleogryllus oceanicus (Le Guillou)

This species is widespread through the Southwest Pacific from northern Austalia and New Guinea eastwards to Hawaii. It is was also recorded from Norfolk Island (Otte & Rentz

1985). At some localities this species was heard singing with *T. marini* (See Fig. 12 for song).

DISTRIBUTION RECORDS. Locs 8, 18, 19.

Teleogryllus marini Otte & Alexander

This species is now known from Queensland, Fiji, and New Caledonia. It lives in very moist grasses and ditches, and is sometimes accompanied by *T. oceanicus*. (See Fig. 12 for song).

DISTRIBUTION RECORDS. Locs 18, 19, 23

MODICOGRYLLINI

Lepidogryllus comparatus (Walker)

Gryllus lepidoides Chopard 1915: 138. *Holotype F*, New Caledonia, Ni, 6 ii 1912. BASEL. NEW SYNONYM.

This species is known from Australia, Norfolk Island, and New Caledonia. It is often found in drier grassy areas, expecially on the west side of the island, sometimes on stony road banks. The song consists of a single beep-like sound with a very rapid pulse rate (see Otte and Alexander 1983 for song).

DISTRIBUTION RECORDS. Locs 3, 9, 30.

Gryllodes sigillatus (Walker)

This cosmopolitan cricket was heard in Noumea and a single female was collected on the east side of the island. This song consists of a rapid train of double-pulse chirps (see Otte and Alexander 1983).

Subfamily NEMOBIINAE

New Caledonia has a diverse Nemobiine fauna, with seven genera and twelve species. Only one genus, *Bobilla*, is found outside New Caledonia (Australia and New Zealand). The genera *Bobilla*, *Koghiella* and *Ignambina* are very similar to *Dictyonemobius* of Lord Howe and Norfolk islands and are here united into the Bobilla Genus Group. *Ionemobius* is very similar to *Thetella* which is widespread through the Pacific, but *Amonomobius* and *Paniella* cannot yet be related to genera elsewhere.

BOBILLA Otte & Alexander

Bullita Gorochov 1986:693. NEW SYNONYM. Type species: *Bullita pacifica* Gorochov 1986: 694.

TYPE SPECIES: *Bobilla bivittata* (Walker)

RECOGNITION OF GENUS. Differs from *Koghiella* in the male genitalia—the apical lobes of the epiphallus bend sharply downwards, have small lumps, and do not extend much beyond the ectoparameres.

Previously this genus was known only from eastern and southern Australia. But it is now also known from New Zealand. Swan 1972 described *Pteronemobius bigelowi* and *P. nigrovus* from New Zealand. Examination of the male genitalia reveals that these are both *Bobilla* species.

Bobilla avita Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Loc. 5, Mt Koghi, West slope of Mt. Bouo, tall forest, 27 ii 1983 (Otte, Alexander, & Cade). PHILADELPHIA.

RECOGNITION. Figs. 14, 15. Table 3. This is the only known member of the genus in New Caledonia. See generic recognition above.

Males: Body color blackish, with orange-brown legs. Head: dorsum black, face black, cheeks black. Pronotum: dorsum dark brown, slightly lighter than lateral lobes, sometimes with a pale patch in each anterior quarter; lateral lobes black. Forewings: dorsum dark brown but with a pale strak along edge of forsal field; lateral field dark brown. Abdomen: dorsum black, venter brown. Fore- and midlegs: uniformly orange-brown. Hindfemora: orange-brown, without oblique stripes. Cerci: orange brown.

Table 2. Comparison of Notosciobia songs. (p/s, pulses per second; ch/s, chirps per second; p/ch, pulses per chirp; KHZ, frequency in kiloHerz. °C, degrees centigrade; solo, single male singing; alt, two males singing simultaneously and alternating.

	p/s	ch/s	p/ch [ch duration]	KHz	°C
Brachytrupinae					
fausta					
Loc 4	78.8	1.38	[0.15]	4.5	24
Loc 4	82.6	1.23		5.2	24
Loc 4	85	1.3	[0.12]	4.7	24
Loc 4	80.9	2.9	[0.06-0.15]	5	24
Loc 4	82.8	1.28	[0.16]	5.2	24
Loc 4	86	1.15	[0.15]	4.6	24
Loc 5	85	0.63	[0.19]	4.2	21.7
Loc 5	82.6	0.5-0.8	[0.16]	4	21.7
Loc 5	86	0.5	[0.17]	3.5	21.7
hirsuta					
Loc 6	91.7	1.27	[0.13]	4.1	26
Loc 6	86	1.95	[0.12]	4.7	26
Loc 6	86	2.28	[0.15]	4.5	26
oubatchia					
Loc 27	64.5	0.55	[0.31]	4.6	24
Loc 27	64.5	0.59	[0.3]	4.5	24
Loc 27	60.9	0.57	[0.31]	3.9	24
oubatchia???					
Loc 25	70.8	0.57	[0.26]	5.2	23
Loc 25	71.7	0.6	[0.23]	5	23
rex					
Loc 13	80.6	0.72	[0.21]	4.2	22
Loc 13	80	0.72	[0.21]	4.2	22
Loc 13	79.8	0.76	[0.2]	4.2	22
[konensis]					
Loc 30	63.1	2.8	3-4	4.2	23
Loc 30	62.9	2.8	3-4	4.2	23
Loc 30	62.1	2.6	3-5	4.5	23
Loc 30	63.4	3.6	3-4	4.2	23
Loc 30	60.7	2.1	3-4	4	23
poya					
Loc 33	16.1	0.72	4	3.3	24.4
Loc 33	16.1	0.7	3-4	3	24.4
Loc 33	15.6	0.22	2	3.5	24.4
Loc 33	19.1	0.7	5-6	3.2	24.4
[parapoya]					
Loc 22	14.3	0.43	3-4	4.2	24
Loc 22	14.3	0.61	3	4.2	24
goipina					
Loc 15	35.8	5.5	2	3.7	21
thiensis					
Loc 6	46.3	9.1	2	4.9	26
Loc 6	43	8.3	2	5	26
Loc 6					

Table 2 (continued)

	p/s	ch/s	p/ch [ch duration]	KHz	℃
nola					
Loc 4	46.9	10.4	2	4	24
Loc 4	51.1	10.1	2	4	24
animata					
Loc 27	47.8	2.87	2	4.8	24
Loc 27	51.6	4.16	2	5.2	24
Loc 27	49.1	4.16	2	4.7	24
canala					
Loc 15	35.6	5.86 solo	2	4	21
Loc 12	35.8	5.73 solo	2	4	22
Loc 11	35.2	4.1-5.7 solo	2	3.8	22
Loc 11	36.5	4.1 alt	2	4	22
Loc 11	33.4	4.4 alt	2	3.8	22
Loc 11	32.8	6.1 solo	2	3.9	22
Loc 11	33.7	5.3 solo	2	3.8	22
Loc 11	25	6.5	2	3.5	22
Loc 11	33.4	3.2 alt	2	4	22
puebensis					
Loc 28	51.6	12.3	2	4.2	24
Loc 28	59.5	11.5	2	4.2	24
Loc 28	52.4	11.8	2	4.3	24
Loc 28	62	12.3	2	4.3	24
GRYLLINAE					
Lepidogryllus comparatus					
Loc 9	172		[0.73]	4.5	24
Loc 3	172		[0.61]	4.3	26

	p/s		pairs/chr	ch/s		
	pt 1	pt 2				
Teleogryllus oceanicus						
Fiji	17.6	30.7	0.57	8.8	4.7	26
Fiji	17.2	27.5	0.63	7.8	4.7	26
Fiji	18.1	33.4	0.54	9.6		26
Loc 19	17.8	29.9	0.6	8.6	5	24
Loc 18	16.1	37.6	0.43	9	5	24
Loc 8	15.6	29.7	0.53	7	5.1	25
Loc 4	19.1	34.4	0.56	9.6	4.8	24
Teleogryllus marini						
Loc 23	18.7	47.3	0.4	9.4	3.3	24
Loc 19	17.2	39.7	0.43	6.8	2.8	24
Loc 19	19.1	45	0.42	8.1	3.5	24
Loc 19	18.1	44.9	0.4	11.1	3.5	24
Loc 19	18.6	45.3	0.41	9.7	3.3	24
Loc 19	19.6	35.3	0.56	9	3.2	24
Loc 18	19.8	49.1	0.4	8.2	3.2	24
Loc 18	20.2	51.6	0.39	6.9	3.3	24
Loc 18	18.6	45.9	0.41	7.4	3.3	24
Loc 19	22.6	34.4	0.66	13.2	3.5	24
Loc 19	23.1	44.2	0.52	10	3.5	24
Loc 18 court	18.1	64.5	0.28	trill	3.2	24
Loc 8	19.9	33.3	0.6	10.7 var	3.5	25

Table 2 (continued)

	p/s	ch/s	p/ch [ch duration]	KHz	°C
OECANTHINAE					
Oecanthus rufescens					
Loc 33	48.7	-	cont.	3.2	24.4
Loc 10	41.3	-	var.	3.6	22
Loc 3	55	-	var.	3.7	26
Loc 6	58.5	-	var.	3.7	26
NEMOBIINAE					
Koghiella bouo					
Loc 4	101	-	[0.93]	5.7	24
Loc 5	90.3	-	[1]	5.6	21.7
Loc 5	91	-	[0.93]	5.3	21.7
Loc 5	94.6	-	[1.74]	5.5	21.7
Koghiella bouo??					
Loc 33	105	-	[0.53]	5	24.4
Koghiella thio					
Loc 6	101	0.25	[0.9]	6	26
Loc 6	99.2	-		6.2	26
Loc 6	99.2	-	[0.93]	5.9	26
Koghiella sp.					
Loc 19	21	0.78	[0.5]	7.2	24
Loc 19	72.8		[0.38]	8	24
Loc 19	70.8	-	[0.49]	7.4	24
Loc 33	70	-	[0.44]	8	24.4
Koghiella sp.					
Loc 10	86	-	[0.81]	5.8	22
Loc 10	86	-	[0.8]	5.7	22
Loc 10	85	-	[0.7]	6	22
Koghiella semibouo					
Loc 5	48.2	0.86	[0.49]	5.5	21.7
Loc 5	47.3	0.83	[0.55]	5.5	21.7
Koghiella caledonica					
Loc 24	64.5	2.42	[0.08]	5.8	24
Amonemobius vexans					
Loc 22	86	2.23	[0.09]	6.5	24
ITARINAE					
Tremellia beta					
Loc 5	86	2.03	[2.1]	3.5	21.7
Loc 5	89	-	[3]	3.5	21.7
Loc 5	87	-	[2.6]	3.5	21.7
Loc 5	86	-	-	3.5	21.7
Tremellia tiwaka					
Loc 30	59.8	1.1	[0.7]	3.8	23
Loc 23	59.1	0.82	[0.84]	3.7	24
Tremellia caledonica					
Loc 5	45	0.13	[2]	3.3	21.7
Loc 5	46			3.5	21.7

Table 2 (continued)

	p/s	ch/s	p/ch [ch duration]	KHz	°C
Tremellia caledonica??					
Loc 22	49.9	-	[1.71]	3.5	24
Loc 10	41.8	-	[1.51]	3.5	22
Tremellia sp?					
Loc 13	33.1	-	[1.74]	3.1	22
Loc 12	33.3	-	-	3.2	22
Tremellia sp?					
Loc 5	24.6	0.8	[0.37]	4.7	21.7
PODOSCIRTINAE					
Calscirtus paniensis					
Loc 27	64.5	0.14	[0.35]	3.2	24
Loc 27	63.4	0.11	[0.41]	3	24
Archenopterus bouensis					
Loc 5	13.2	-	[1.5-2.0]	4	21.7
Loc 5	12.9	-	[1.3+]	4.1	21.7
Podoscirtinae 1					
Loc 5	24.2	0.17	[0.47]	4.2	21.7
Podoscirtinae 2					
Loc 30	22.9	0.25	[0.45]	4.5	23
Loc 16	22.2	0.31	[0.47]	4.5	21
Loc 10	23.5	-	[0.62]	4.2	22
Loc 10	23.7	0.22	[0.6]	4.3	22
Podoscirtinae 3					
Loc 4	26.2	1.1	[0.47]	5.7	24
Loc 5	25.5	0.9	[0.46]	4.8	21.7
Podoscirtinae 4					
Loc 4	36.9	0.29	[0.23]	4.9	24
Loc 4	38.7	0.17	[0.21]	4.8	24
Podoscirtinae 5					
Loc 30	33.1		[0.15]	5.3	23
Loc 19	33.4	0.32	[0.22]	5	24
Loc 19	38.2	-	[0.12]	5	24
Loc 19	36.2	-	[0.16]	4.7	21
Loc 19	36.8	-		4.7	21
Loc 9	34.4	0.32	[0.21]	4.4	21
Loc 9	32.3	-	[0.17]	4.2	21

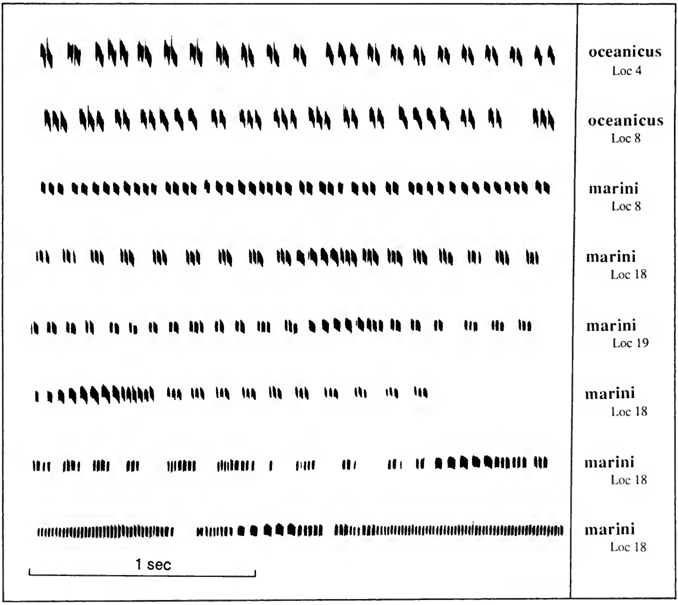


FIG. 12. *Teleogryllus* songs. *1st and 2nd songs*: normal *oceanicus* songs. *3rd song*: atypical *marini* song which appears to be more similar to *oceanicus* songs but the low frequency indicates that it belongs to *marini*. *4th, 5th, and 6th songs*: typical *marini* calling songs. *7th song*: calling song transition to courtship song. *8th song*: presumed courtship song. (Scale = 1 second).

Females: colored like males. Forewings very short, longest along side of body, overlapping medially, dorsal field pearly along posterior margin.

BIOLOGY. Collected in leaf litter and along a trail in a tall rain forest.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratypes*: same data as holotype, 2M 4F, PHILADELPHIA & ANN ARBOR.

Bobilla pacifica Gorochov

Bullita pacifica Gorochov 1986: 694. *Holotype M*, Oceania, New Caledonia (no additional data). LENINGRAD. Type not examined.

RECOGNITION. Fig.15B. This species differs from *avita* in the male genitalia.

Gorochov (1986) provides the following description: Male (holotype). In size rather small

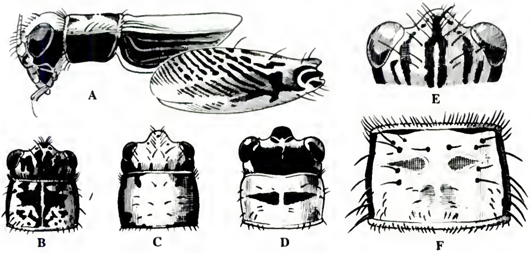


FIG. 13. Nemobiinae (holotypes). **A**, *Koghiella parabouo*. **B**, *Koghiella bouo*. **C**, *Ionemobius alliciens*. **D**, *Koghiella caledonica* head. **E**, *Koghiella caledonica* pronotum.

Table 3. Morphological comparison of Nemobiinae species. See Methods for abbreviations.

	No. file teeth	BL	FL	FWL/PL	TL/FL	OL/FL	CL/FL
Bobilla avita							
Loc 5 M (n=3)	106-107	6.5-7.5	4.3-4.5	2.2-2.3	0.80-0.82	-	ca. 0.95
Loc 5 F (n=2)	-	6.1, 7.3	4.2,4.3	ca. 0.55	ca. 0.8	0.65, 0.66	-
Koghiella bouo							
HM	57	7.3	4.6	-	0.68	-	-
Koghiella semibouo							
HM	87	7	4.3	2	-	-	0.8
PM	87	7.7	4.6	2	-	-	-
Koghiella parabouo							
HM	94	9.7	5.4	2.1	0.7	-	-
PF		8.7	5	-	-	0.97	0.85
Koghiella thio							
M (n=3)	90-92	7.3-7.8	4.2-4.8	-	ca. 0.7	-	0.7-0.9
F		7.8	4.5	-	-	0.87	0.8
Koghiella caledonica							
M Loc 10	84	6.9	3.8	2.1	-	-	0.74
M Loc 33	80	8.1	4.7	1.85	-	-	0.75
M Loc 24	84	7.8	4.5	1.9	-	-	0.72
F Loc 10	-	8.3	4.5	-		0.85	0.76
F Loc 33	-	7.4	4.9	0.48	-	0.81	-
F (n=3) Loc 24	-	7.9-8.7	4.3-4.9	0.42	-	0.85-1.1	0.78-0.91
Ignambina oubatchia							
HM	106	7.7	4.6	2.3	0.75	-	0.83
PM	-	7.9	4.2	2.2	-	-	-
PF	-	7.3	4.6	0.33	-	0.8	0.8
Ionemobius alliciens							
HM (n=3)	55-58	7.7-8.9	4.6-4.8	1.7-1.8	-	-	0.6-0.7
PF		8.5	5.3	0.26	-	0.87	0.75
Amonemobius caledonicus							
HM	71	7.5	4.8	2.3	0.85	-	-
PF	-	6.6	4.6	-	0.77	0.63	-

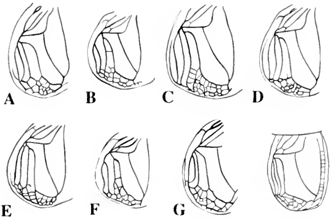


FIG. 14. Nemobiinae male forewings (holotypes). A, *Bobilla avita.* B, *Koghiella bouo.* C, *Koghiella parabouo.* D, *Koghiella thio.* E, *Koghiella caledonica.* F, *Ionemobius alliciens.* G, *Amonemobius vexans.* H, *Apteronemobius gusevae* (from Gorochov 1986).

for tribe. The color of the body is chestnut brown, unicolorous, only the disc of the pronotum has poorly developed bright markings [his fig. 30]. The wing covers are also chestnut brown, but the dorsal survace along the fold is with a very narrow bright streak. The legs are also brown, monochrome, only on the rear femora have barely noticeable oblique lines. The wing veins and the male genitalia as are in [his figs 5-7, 30]. Body length 6 mm; pronotal length 1.5 mm; forewing length 3.3 mm; hindfemur length 4.4 mm.

SPECIMENS. *Holotype* M, LENINGRAD.

KOGHIELLA n. gen.

TYPE SPECIES: *Koghiella bouo* Otte, n. sp.

RECOGNITION OF GENUS. Figs. 13-18. Table 3. Most similar to *Bobilla* (of Australia, New Zealand and New Caledonia), *Ignambina* (New Caledonia) and *Dictyonemobius* (of Norfolk and Lord Howe islands). Unlike *Bobilla* the apical epiphallic lobes extend well beyond the ectoparameres and are not turned downwards. Unlike *Ignambina* the epiphallus is bifurcate at the apex.

Body color dark brown to blackish on sides of body, variegated pale and dark brown on dorsum of pronotum and abdomen. Head with four broader and two narrower longitudinal dark bands on occiput and vertex, with long stout black bristles. Face usually with two parallel dark stripes on face which diverge from one another ventrad, following the antennal sockets and with a broad dark area descending from the eyes onto the mandibles. Pronotum: Dorsum reddish brown to pale brown, often with dark maculations; lateral lobes blackish. Forewings: without a mirror; with one harp vein, diagonal vein and Cu_2 in chordal area share an exclusive common stem; dorsal field generally brown to dark brown, veins in apical area, chordal area and basal areas often very pale; lateral field dark. Fore- and midfemora pale, with larger dark areas generally basal to large black bristles; tibiae banded with dark brown; fortibiae with large outer and no inner tympanum; fore- and midtibiae with two and three apical spurs respectively. Hindfemora with dark oblique stripes on outer

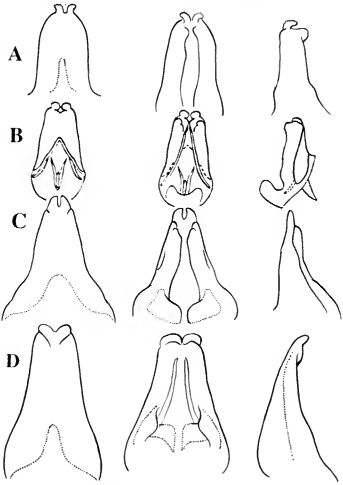


FIG. 15. Nemobiinae male genitalia (holotypes). A, *Bobilla avita*. B, *Bobilla pacifica* (from Gorochov) C, *Koghiella bouo*. D, *Koghiella parabouo*.

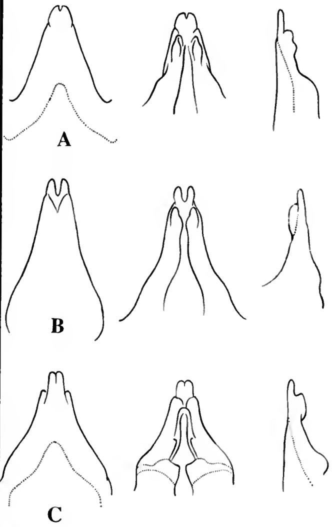


FIG. 16. Nemobiinae male genitalia (holotypes). **A,** *Koghiella semibouo.* **B,** *Koghiella thio.* **C,** *Koghiella caledonica.*

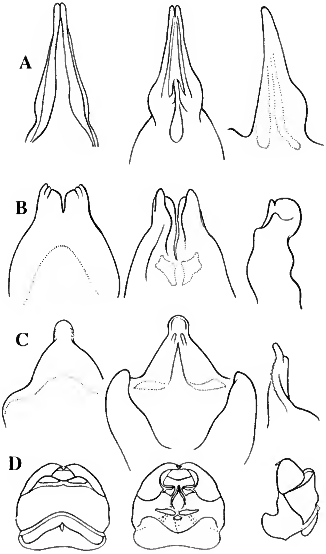


FIG. 17. Nemobiinae male genitalia (holotypes). **A,** *Ionemobius alliciens.* **B,** *Amonemobius vexans.* **C,** *Ignambina oubatchia.* **D,** *Apteronemobius gusevae.*

and upper faces. Hindtibiae with dark to black bands on posterior face between the spurs; with four inner and five outer subapicals. Abdomen: pale brown to reddish brown, speckled with darker spots, lateral surface of tergites black.

Females: Size and color like males; forewings shorter than pronotum, bristly, transversely truncated (appears to be a tergite), meeting at midline, longest along side of body.

Koghiella bouo Otte, n. sp.

TYPE. *Holotype M,* New Caledonia, Loc. 5, Mt Koghi, West slope of Mt Bouo, tall forest, 27 ii 1983 (Alexander, Cade & Otte). PHILADELPHIA.

RECOGNITION. Figs. 13B, 14B, 15. Table 3. Most easily confused with *semibouo* and *thio,* but apex of epiphallus with a narrow U-shaped cleft which is as deep as the terminal lobes are wide. Stridulatory file with fewer than 70 teeth (more than 80 teeth in *thio* and *semibouo*).

Males: Head: dorsum marked as shown in figure. Face with two parallel dark stripes on fron which diverge towards clypeus, with broad dark area descending from eyes onto mandibles; central portion of clypeus and labrum ivory colored; cheeks dark brown to black. Promotum: dorsum marked as shown in figure; lateral lobes black. Forewings: dark brown, veins 2A and 3A, base of stridulum, chords and apical veins pale. Abdomen: dorsum variegated dark brown and pale brown, but mostly dark brown; venter medium brown with indistinct light and dark bands. Fore- and midlegs: femora pale with large dark brown patches, especially at base of black setae; tibiae banded with dark brown. Hindfemora: with numerous dark brown oblique stripes on upper and outer faces. Cerci: medium brown.

Koghiella parabouo Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Mt. Koghi, west slope of Mt Bouo, tall forest, 27 ii 1983 (Alexander, Otte & Cade #5). PHILADELPHIA.

RECOGNITION. Figs. 13A, 14C, 15D. Table 3. Very similar to *bouo and semibouo* but apical cleft of epiphallus wide, V-shaped and entire structure bending downwards (in side view). Body also larger than these two species.

Males: Head: dorsum with 4 major longitudinal bands and 2 small ones lateral to these; face with two dark bands diverging ventrad; cheeks dark brown. Pronotum: dorsum pale brown with symmetrical dark brown spots and markings; lateral lobes dark brown to black. Forewings: dorsum dark brown with pale veins in apical, chordal and basal areas, lateral field dark brown. Abdomen: dorsum pale brown with dark spots, markings becoming larger laterally; venter lighter brown, with indistinct brownish areas, subgenital plate dark brown. Fore- and midlegs with large dark and pale areas. Hindfemora with with stong oblique dark brown stripes on upper and outer faces.

Female: Similar to male in size and color.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratypes:* Same data as holotype, 1F, PHILADELPHIA. 34 km west of Canala, 1M, ANN ARBOR

Koghiella semibouo Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Loc. 5, Mt Koghi, West slope of Mt Bouo, tall forest, 27 ii 1983 (Alexander, Cade, and Otte). PHILADELPHIA.

RECOGNITION. Figs. 16A. Table 3. May be confused with *bouo*; differs in having a small apical cleft on the epiphallus and in having more than 80 file teeth.

Males: Head: vertex and occiput without distinct dark bands (similar to *bouo*). Face similar to bouo; cheeks dark brown to black. Pronotum: dorsum not strongly variegated, much lighter than lateral lobes; lateral lobes blackish. Abdomen: dorsum variegated dark and pale brown, becoming blackish along lateral margins; venter brown with 4 longitudinal rows of darker brown markings. Fore- and midlegs: femora pale brown with a distal dark brown ring, and with dark brown spots at bases of bristles; tibiae with 3 dark crossbands only on upper face. Hindfemora: orange brown with dark brown oblique stripes on upper and outer faces. Cerci medium brown.

Females not known.

BIOLOGY. Collected along grassy trails in tall rainforest.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratype*: same data as holotype, 1M, PHILADELPHIA.

Koghiella thio Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Loc. 6, 12 km SE Thio, forest along beach, 28 ii 1983 (Alexander, Cade & Otte). PHILADELPHIA.

RECOGNITION. Figs. 14D, 16B. Table 3. Distinguished from other members of the genus by the male genitalia—the apical lobes are widely separated by a deep U-shaped cleft. Also differs from the very similar bouo in having more than 85 file teeth.

Males: Body highly speckled. Dorsum of body (exept forewings) pale with black spots, side of head, pronotum and forewings black. Head: vertex and occiput with 6 indistinct slightly reddish longitutinal bands; most prominent aspect are the rows of heavy black bristles, each emerging from a brown to dark brown spot. Median ocellus raised above plain of the forehead and facing forwards. Face with a broad dark band descending from eyes to ends of man-

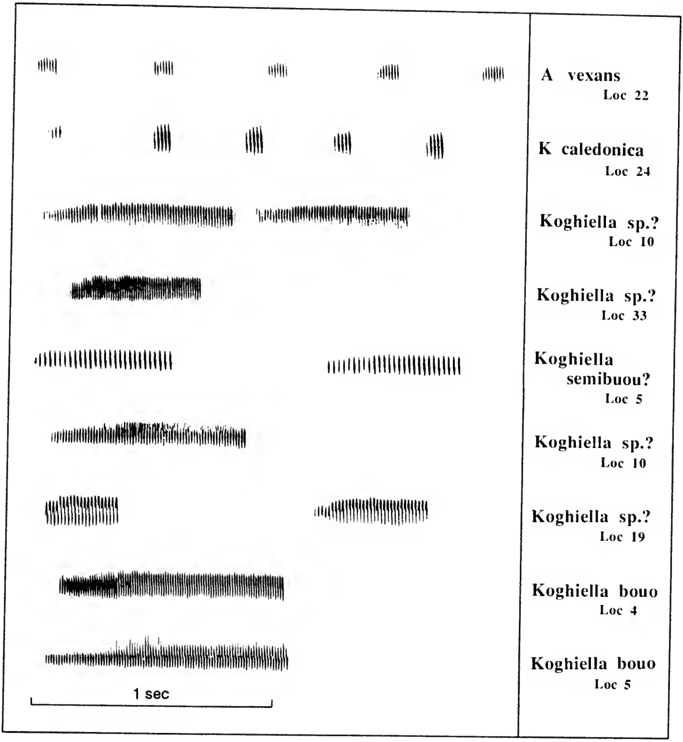


FIG. 18. Nemobiinae songs (scale = 1second).

dibles; frons with 2 dark bands descending towards clypeus then bending laterally. Upper lobe of clyeus with 3 dark brown markings, one medial, two lateral; lower lobes with two basal dark brown marks then ivory. Labrum pale centrally, brownish laterally. Cheeks medium to dark brown up to top of eyes, then pale. Pronotum pale brown; slightly darker on MAPs, with numerous small brown spots, each at the base of a bristle. Forewings: dorsum brown, but veins 2A, 3A, chords, and apical veins and Cu_1 and M veins pale; lateral field dark brown. Abdomen: dorsum with numerous fine black setae; pale brown with small and large spots forming a row across each tergite: tergite becoming dark brown on lateral face. Fore- and midfemora: very pale, but with dark brown marks mainly proximal to each black bristle, and dark brown at apex. Tibiae brown to dark brown, forming 3 indistinct bands. Hindlegs: femora ivory with numeros dark brown oblique stripes upper and outer faces; tibiae dark brown with pale areas around bases of spurs. Cerci: pale to medium brown.

Females: Colored like male. Forewings very short, meeting at midline, posterior border with heavy bristles like tergites which follow.

BIOLOGY. Collected in coastal forest along the beach, especially among rocks and litter along a small stream running through the forest.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratypes*: same data as holotype, 2M 1F, PHILADELPHIA.

Koghiella caledonica (Chopard)

Dictyonemobius caledonicus Chopard 1970: 285. *Holotype M*, New Caledonia, Hienghene, Grotte, 5 ix 1965. VIENNA. Type exa-mined.

RECOGNITION. Figs. 13D, 14E, 16C. Table 3. Very similar to *thio*, but epiphallus with very narrow, closely juxtaposed apical lobes; also differs in having fewer than 85 file teeth.

Males: Head: dorsum with indistinct to moderately distinct brown bands. Forewings dar brown, but pale on veins 2A, 3A, base of stridulum, some apical veins, especially on extreme outer margins of apical area. Abdomen: dorsum mostly dark brown with pale spots. Legs like *thio*.

BIOLOGY. Collected along a road which ran through the forest.

SPECIMENS. *Holotype* M, VIENNA. About 25 km west of Canala, along road through forest, 1 iii 1983 (Alexander, Cade and Otte) 1M, PHILADELPHIA. 28 km west of Canala, 1 iii 1983 (Alexander) 1F, ANN ARBOR. Loc. 16, 2M, ANN ARBOR.

IGNAMBINA Otte, n. gen.

Ignambina oubatchia Otte, n. sp.

RECOGNITION OF GENUS. Very similar to *Koghiella*. Differs from all other species in having a uniquely shaped epiphallus: the apical lobe not bifurcate and epiphallus very wide at base and with small blunt spines on dorsal face.

Ignambina oubatchia Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, ca. 17 km SE of Oubatche, coastal forest, 6 iii 1983 (Alexander, Otte and Cade # 27). ANN ARBOR.

RECOGNITION. Fig. 17C. Table 3. Very similar to *Koghiella caledonica*. Differs from all other species in having a uniquely shaped epiphallus.

Males: In shape and color largely indistinguishable from *caledonica*.

SPECIMENS. *Holotype* M, ANN ARBOR. *Paratypes*: Same data as holotype, 2M, ANN ARBOR and PHILADELPHIA.

AMONEMOBIUS n. gen.

TYPE SPECIES: *A. vexans* Otte, n. sp.

RECOGNITION OF GENUS. Ectoparameres of male genitalia extending beyond epiphallus; epiphallus with a deep median cleft (Fig.). Dorsum of head mostly pale but with occiput with four small black stripes; region posterior to eyes black; dorsum of pronotum largely pale but with a dark patch in each corner. Foretibiae with a large opening only on the outer face.

Amonemobius vexans Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Amoa river valley, 8.4 km west of main coastal road near Poindimié, 3 iii 1983 (Alexander, Cade & Otte). PHILADELPHIA.

RECOGNITION. Figs. 14G, 17B. Table 3. *Male*: Body color very pale with dark brown to black patches on the head, pronotum, abdomen and legs. Head: dorsum marked as in Fig. ; face largely ivory but frons with two brown streaks descending between the antennae then curving laterally halfway between the clypeus and the antennal sockets and with a central dark mark which carries overy onto the clypeus; cheeks with a broad black band descending from the lower margin of the eye onto the base of the mandible. Pronotum: dorsum ivory and black (Fig.); lateral lobes blackish. Forewings: dorsum dark brown but ivory at junctions of chords and stridulum and around distal ends of chords; lateral field dark brown. Abdomen: dorsum pale with some black spots and markings; venter pale brown. Fore- and midlegs: femora ivory colored and with two broad dark bands; tibiae with two dark bands. Hindlegs: femora ivory with three dark bands in distal two thirds; tibiae pale with a dark stripe between the spurs, and with two dark cross bands in the basal third. Cerci light brown.

SONG. Not known.

HABITAT. Found on banks along a road through the forest in the Amoa Valley.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratype*: 17 km southeast of Oubatche, 6 iii 1983 (Alexander, Cade & Otte) 1F, ANN ARBOR.

APTERONEMOBIUS Chopard

Apteronemobius Chopard 1929: 29. Type species: A. longipes Chopard 1929: 29, by monotypy.

Paora Gorochov 1986:692. Type species: *Paora gusevae* Gorochov 1986. New synonym.

Apteronemobius gusevae (Gorochov)

Paora gusevae Gorochov 1986:692. *Holotype M*, New Caledonia (no other data). LENINGRAD. NEW COMBINATION.

Recognition. Comparison of the male genitalia of Apteronemobius darwini (Otte and Alexander 1983 Fig. 147A) and Gorochov's Paora gusevae(Fig. 17D) shows that this species belongs to Aperonemobius.

PANIELLA n. gen.

TYPE SPECIES: *Ignambina oubatchia* Otte, n. sp.

RECOGNITION. See *P. apterus* below.

Paniella apterus (Chopard)

Pronemobius apterus Chopard 1915: 133. Types: 2M. New Caledonia, summit of Mont Panié, 1600 m, 28 vii 1911. BASEL and PARIS.

NOTES ON HOLOTYPE. Foretibiae without a tympanum. Fore- and midtibiae with 2 and 3 apical spurs, respectively. Hindfemora with only 3 inner and 3 outer subapical spurs.

Thetellini

IONOMOBIUS n. gen.

TYPE SPECIES: *A. vexans* Otte, n. sp.

RECOGNITION OF GENUS. Epiphallus very slender and tapering, similar to *Thetella*. Differs from *Thetella* is having two and three apical spurs on the Fore- and middle tibiae (2 and 2 in *Thetella*), and in having a black head. Foretibiae with only a large outer tympanum.

RELATIONSHIP. The genitalia of *Ionemobius* and *Thetella* are so similar that the two perhaps should be treated as members of the same genus.

Ionemobius alliciens Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, about 12 km southeast of Thio, forest along beach, 28 ii 1983 (Alexander, Cade & Otte #6). PHILADELPHIA.

RECOGNITION. Figs. 13C, 14F, 17A. Table 3. Epiphallus very slender. Dorsum of head black. Dorsum of pronotum pale but muscle attachment plates brown. *Males:* Body color pale but with dark brown on head. Head: occiput and vertex black but with a pale band which runs between the posterior margins of the antennal sockets; forehead black; face mostly dark brown on frons, but with a pale area beneath each antennal socket and with a dark brown band denscending from each eye to the mandibles; cheeks ivory colored. Pronotum: dorsum very pale but muscle attachements plates light brown; lateral lobes ivory colored in anterior two-thirds and dark brown in posterior third. Forewings: dorsal field medium to dark brown, but pale from the harp veing to the M vein; lateral field brown to dark brown. Abdomen: anterior segments of dorsum entirely dark brown, last six segments variegated dark brown and ivory, but in a female has four rows of dark spots, two rows near the midline and two rows near the margins of the tergum. Fore- and midlegs: femora ivory with faint large brown markings on outer faces; tibiae uniformly pale brown. Hindlegs: femora pale with brown oblique stripes on upper and outer faces; these become darker posteriorly and coalesce to for a broad dark brown band at the two-thirds point, knees also brown.

Females: Similar to male in size and body color. Forewings consist of small hemicircular pads located on the shoulder of the mesonotum and not overlapping medially. In females the abdomen is largely pale but has four rows of dark spots on the tergum, two near the midline and two laterally. Ovipositor nearly 0.9 times as long as Hindfemora.

SONG. Not known. The surf was too loud to permit tape recordings of this species.

HABITAT. Collected along a small stream and along the stony shoreline among wet stones and debris.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratypes*: same data as holotype, 4M 1F, PHILADELPHIA and ANN ARBOR.

FIKOLA Gorochov

TYPE SPECIES: *Fikola fusca* Gorochov 1986.

RECOGNITION OF GENUS. The following description is taken from Gorochov (1986). "Forewings of female very short; rear border with characterist curve, lateral field convex; forewing color black, with a white streak along the rear border. Foretibiae lacking a tympanal opening. Hindtibiae with four pairs of rather long spines. Ovipositor lacking noticeable serrations, but with narrow apical valves.

Fikola fusca Gorochov

Fikola fusca Gorochov 1986: 694. *Holotype F*, New Caledonia, Noumea (Mt. Koghi) 14 x 1977 (J. Balogh). HUNGARIAN MUSEUM.

RECOGNITION. The following description is from Gorochov (1986): Size not large. Body color dark brown, almost black. Head black, with two very bright streaks on the sides in the middle of the eye and with a yellow-orange triangle in the distal part of the frontal suture. On the rear borders of the tergites of the abdomen are some pale sections. Legs rust-colored, unicolorous. Ovipositor is 1.7 times shorter than the rear femur, slighly bent upwards. Measurements (mm): BL, 7; PL, 1.8; FWL, 0.7; FL, 5; ovipositor, 3.0.

SPECIMENS. *Holotype* F, HUNGARIAN MUSEUM. *Paratypes*: same data as holotype, 1F, HUNGARIAN MUSEUM; 1F, LENINGRAD.

ORINTIA Gorochov

TYPE SPECIES: *Orintia incrustata* Gorochov

RECOGNTION OF GENUS. Gorochov (1986) gives the following description of this genus: Body stocky. Forewings absent in females, hindwings represented by small blades at the the sides. Head large, a little wider than other parts

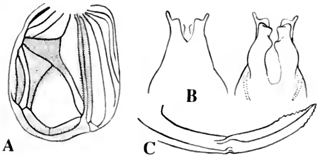


FIG. 19. *Anaxipha caledonica.* (holotype). **A**, male forewing. **B**, male genitalia (dorsal and ventral aspects). **C**, female ovipositor.

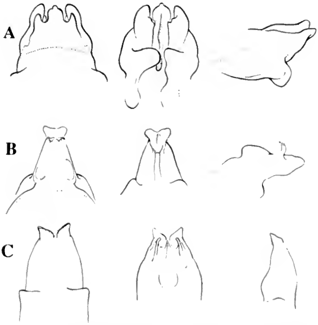


FIG. 20. Male genitalia (holotypes). **A**, *Caltathra paniki.* **B**, *Proturana subaptera.* **C**, *Aphonoides ouveus.*

of the body. Legs rather short and thick. Front legs with small tympanal openings on the outer side. Hindlegs with three pairs of spurs. Spines on the hind basitarsus rather short. Ovipositor with narrow apical valves, rather long and more or less straight. Color variegated."

Orintia incrustata Gorochov

Orintia incrustata Gorochov 1986: 698. *Holotype F,* New Caledonia (no further data). LENINGRAD.

RECOGNITION. Gorochov gives the following description of the holotype: "Size small. Coloring of head chestnut borwn and with characteristic markings of dark and greenish yellow spots above. Antennae are cinnamon colored, but the segments are white with two proximal sections of brown. Pronotal disc yellowish with two dark spots; lateral lobes dark brown. Legs pale, with dark spots. Color of hindleg shown in [his] fig. 28. Abdomen brown below, with scattered marks of dark and pale yellow spots above. [Measurements (mm)]: BL, 5.5; PL, 1.2; FL, 4.2; OL, 3.2."

SPECIMEN. *Holotype* M, LENINGRAD.

Table 3. Comparison of Nemobiinae species. See Methods for abbreviations.

TRIGONIDIINAE

This subfamily is very poorly represented in New Caledonia and we now know of only two genera and two species which inhabit the islands and one of these is widespread through the Pacific.

Trigonidomorpha sjöstedti Chopard

Trigonidomorpha sjöstedti Chopard 1925: 40. *Holotype M,* Australia, Queensland, Cedar Creek (Mjöberg). STOCKHOLM. Type examined.

This species is very widely distrubed over in the Pacific islands. It is now known from New Guinea, Australia, Norfolk Island and Hawaii.

RECOGNITION. See Otte & Alexander 1983, p. 223 and accompanying figures.

SPECIMENS. Loc 4, 3M 1F; Loc 19, 3M 1F; Loc 29, 2M.

Metioche vittaticollis Stal

Chopard 1970: 287 records this species from: lower reaches of Tshamba River 16 vii 1965, Koh, 29 vii 1965. Noumea, 21 iii 1965. These specimens are probably *Trigonidomorpha sjöstedi.* See Otte and Alexander 1983 for description and figures.

Metioche flavipes Saussure

Chopard 1970:287 records this species from the coast near Dumbea, 17 vii 1965; Noumea 16 vii 1965; Koh 29 vii 1965. These specimens are probably *Trigonidomorpha sjöstedi*.

Anaxipha caledonica Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, grottoes area about 7 km west of Koumac, 7 iii 1983 (Alexander, Cade and Otte). PHILADELPHIA.

RECOGNITION. Fig. 19. Table 2. A pale green species with genitalia as figured.

Pale green in life (ivory colored when preserved in alcohol; dorsum of head and pronotum orange brown. Face entirely pale. Pronotum: dorsum pale over most of central portion, becoming darker brown towards all four sides; lateral lobes pale in lower half, brownish in upper half. Forewings: dorsal field dark brown along M vein and between mirror and stridulum; lateral field pale, with a dark stripe along the dorsal margin. Abdomen entirely pale green (in life). Foretibiae with only a large outer tympanum. All legs pale, unicolorous (green in life).

HABITAT. This species was singing during the day in the trees in a forested ravine near some grottoes. Some were singing in low trees others were higher in the trees.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratypes*: same data as holotype, 2M 1F, PHILADELPHIA and ANN ARBOR.

PHALANGOPSINAE

CALTATHRA Otte, n. gen.

TYPE SPECIES: *C. panaki* Otte, n. sp.

RECOGNITION OF GENUS. Entirely wingless. Body color mottled dark brown and ivory, legs strongly banded. Dorsum of head with brown bands; face dark brown with a white band descending from median ocellus to labrum. Pronotum: dorsum patterned; lateral lobes mostly brown. Forewings and hindwings absent. Abdomen mottled with indistinct brown and ivory markings. Fore- and midfemora with 3 dark bands. Fore- and midtibiae with 2 and 3 apical spurs respectively. Hindfemora with patches of dark brown; tibiae with 4 dark bands; with 3 inner and 4 outer subapical spurs.

Caltathra panaki Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, road to Panaki from Koné, mountain forest above Koné, 7 iii 1983 (Alexander, Otte & Cade #30). ANN ARBOR.

RECOGNITION. Figs. 20A, 22C, 25D. Table 4. *Male:* Body color mottled dark brown and ivory, legs strongly banded. Head: dorsum with 8 longitudinal brown bands (2 median ones separated by a very thin pale line); forehead between the three ocelli dark brown, with bristles; face dark brown, with a white band descending from median ocellus to labrum; cheeks ivory colored behind eyes and a pale vertical streak extends and narrows from eye to base of mandible. Pronotum: dorsum patterned; lateral lobes mostly brown, but with a pale spot in lower front corner and a small spot in middle tope (adjacent to MAPs). Forewings and hindwings absent. Abdomen mottled with indistinct brown and ivory markings. Fore- and midlegs: femora with 3 dark bands, tibiae with 4 dark bands. Hindlegs: femora with 6 or 7 large patches of dark brown; tibiae with 4 dark bands; with 3 inner and 4 outer subapical spurs; on inner side all spines located above the spurs, on the outer side they are also located between the upper three spurs.

SPECIMENS. *Holotype* M, ANN ARBOR.

Caltathra dubia Chopard, n. comb.

Endacusta dubia Chopard 1915: 146. *Holotype F*, Yaté, 15 iii 1912. BASEL.

Endotaria steinmanni Gorochov 1986:699. *Holotype F*, New Caledonia (Mt. Koghi). HUNGARIAN MUSEUM. NEW COMBINATION. Type not examined.

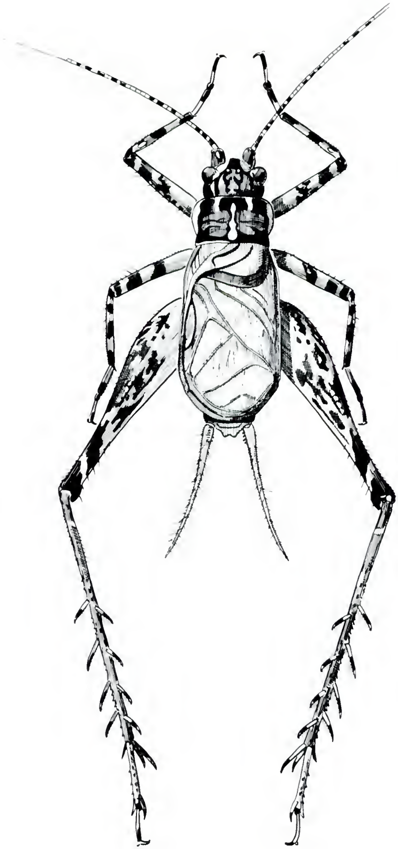


FIG. 21. *Tremellia alpha* male.

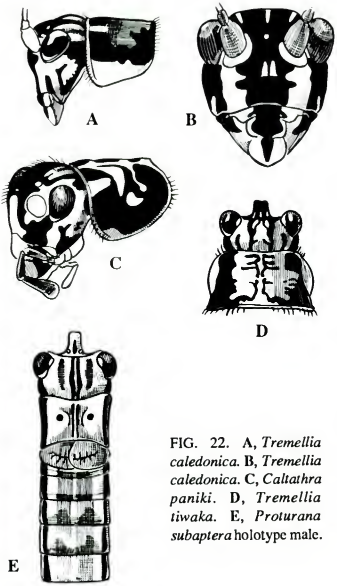


FIG. 22. A, *Tremellia caledonica.* B, *Tremellia caledonica.* C, *Caltathra paniki.* D, *Tremellia tiwaka.* E, *Proturana subaptera* holotype male.

Two females collected at Loc 5 are believed to belong to this species. Occiput with 4 broader pale longitudinal bands (plus a very narrow median pale line) which almost reach the pronotum; vertex with 4 pale bands. Otherwise coloration similar to *panaki.*

SPECIMENS. Loc 5, 2F, PHILADELPHIA & ANN ARBOR.

ITARINAE

TREMELLIA Stal

Tremellia Stal 1877: 47. Type species: *Tremellia spunca* Stal, Philippines, by monotypy.

Pseudotrigonidium Chopard 1915:152. Type species: *Tremellia sarasini* (Chopard). New Caledonia. Synonymized by Chopard 1968: 364.

RECOGNITION. Figs. 21-25, 45. Table 4. Dorsum of body dark brown, venter ivory, sides of body dark brown in upper half, ivory below. Pronotum: dorsum marked as in Fig. 21; lateral lobes blackish in upper half pale in lower half. Forewings: covered with fine pubescence; dorsum gray to dark brown, usually with a somewhat mottled appearance; lateral field pale to dark brown; area between R and M broad, with 10 or more regularly spaced cross veins—this area has a pearly white streak along its middle. Hindwings about one half to two thirds as long as forewings. Fore- and midlegs: Femora and tibiae banded somewhat as in Fig. 21; foretibiae with only an inner tympanum; with 2 and middle tibiae with 2 apical spurs. Hindfemora marked as in Fig. 21. Hindtibiae with 4 inner and 4 outer subapical spurs, and with 3 inner and 3 outer apical spurs.

Tremellia sarasini (Chopard)

Pseudotrigonidium sarasini Chopard 1915:153. *Holotype M*, New Caledonia, Foret du Mont Panié, alt. 500 m, 27 vi 1911. BASEL. Type not examined but original figures adequate for diagnosis.

RECOGNITION. Lateral projection on male epiphallus as in Fig. 24H.

SPECIMENS. *Holotype* M, BASEL.

Tremellia tiwaka Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Loc 23, Tiwaka River, ca. 5 km west of main north-south road, near Poindimié, 3 iii 1983 (Alexander, Cade and Otte). PHILADELPHIA.

RECOGNITION. Figs. 22D, 23D,E, 24G, 45. Table 4. Easily distinguished from other species by the male genitalia. In the females the forewings are much longer than in *beta.*

Males: Head: face and cheeks similar to *alpha.*

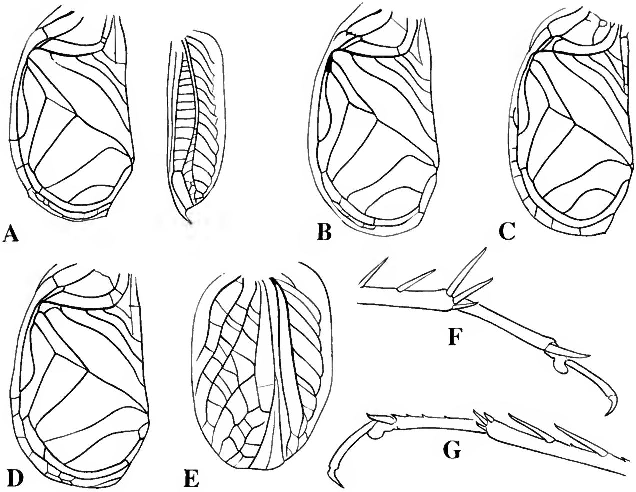


FIG. 23. *Tremellia*: holotypes: A-E, forewings; F, G, hind tibia and tarsus. A, *alpha* (dorsal and lateral aspects). B, *caledonica*. C, *beta*. D, *tiwaka*. E, *tiwaka* female. F, inner face. G, outer face.

Table 4. Comparison of Tremellia species. See Methods for abbreviations.

	No. file teeth	BL	FL	CL	FWL/PL	TL/FL	OL/FL
Caltathra panaki							
HM	0	13.5	11.2	10.0+	-	0.87	-
Caltathra dubia							
Loc 5 F	0	11.8	9.5	6.5	-	0.84	0.68
Tremellia caledonica							
HM	77	12	10	ca. 5	4.1	1	-
Tremellia alpha							
HM	76	10.2	9.7	5.2	3.9	1.04	-
Tremellia beta							
HM	80	13	10.5	6.5	3.5	1.03	-
PF	-	10	8.3	5.4	0.4	0.98	0.57
Tremellia tiwaka							
HM	70	11.5	9.5	-	4.5	-	
PM	-	10	8.5	4.9	-	-	-
PF	-	9		4.9	2.9	-	0.43

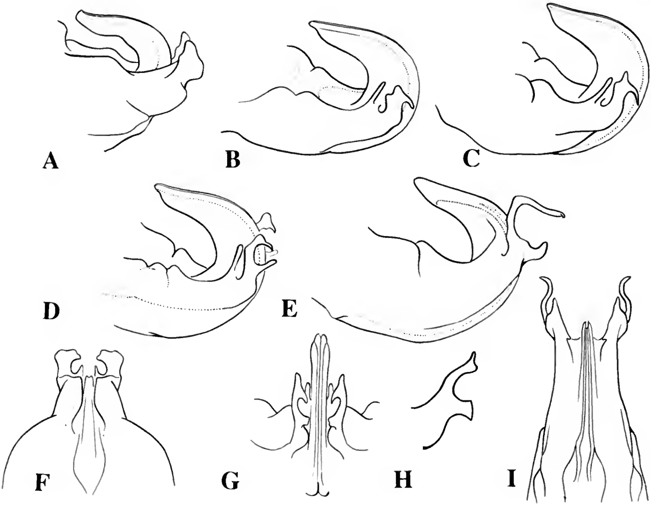


FIG. 24. *Tremellia* male genitalia (mainly lateral aspect)(holotypes). **A**, *beta*. **B**, *tiwaka* holotype. **C**, *tiwaka* loc 30. **D**, *alpha*. **E**, *caledonica*. **F**, *beta* (ventral aspect). **G**, *tiwaka* (ventral aspect). **H**, *sarasini* (from Chopard). **I**, *caledonica* (ventral aspect).

Pronotum: Dorsum as figured; lateral lobes black above, pale below. Forewings: dorsum pale brown, somewhat mottled; lateral field pearly white between the R and M veins; the latter veins are dark brown, other veins pale. Abdomen: dorsum variegated brown and ivory; venter with two rows of faint brown spots.

Females: marked like males; hindwings about 0.66 times length of forewings; antennae ca. 105 mm long.

SPECIMENS. *Holotype* M, PHILADELPHIA. Loc. 30, 3M 1F, PHILADELPHIA & ANN ARBOR.

Tremellia alpha Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Loc. 16, ca. 40 km west of Houailou, hillside forest, 2 iii 1983 (Alexander, Cade, and Otte). PHILADELPHIA.

RECOGNITION. Figs. 21, 23A, 24D. Table 4. Distinguished from other species by the male genitalia.

Males: Dorsum of body dark brown, venter ivory, sides of body dark brown in upper half, ivory below. Head: dorsum banded as in Fig. ; face with a broad median dark band descending face onto ldabrum; frons above bottom of antennal sockets entirely dark, otherwise ivory. Pronotum: dorsum marked as in Fig. 21; lateral lobes blackish in upper half pale in lower half. Forewings covered with fine pubescence dorsum dark brown with a somewhat mottled appearance; lateral field dark brown but area between R and M broad, with 10 or more regularly spaced

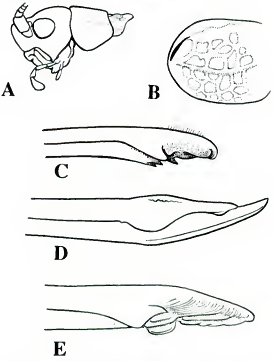


FIG. 25. A, *Proturana subaptera* head, pronotum and forewing. B, *Proturana subaptera* forewing. C, *Tremellia tiwaka* ovipositor. D, *Caltathra paniki*. E, *Matuanus elegans*.

cross veins—this area has a pearly white streak along its middle. Abdomen: dorsum mostly dark brown with regular pattern of paler spots. Fore- and midlegs: femora and tibiae banded dark brown and ivory. Hindfemora: banded dark brown and ivory, outer face with 3-4 horizontal bands made up of smaller oblique stripes. Cerci pale brown. Hind tibiae: outer margin with numerous small spines, inner one only above the first spur. Hind basitarsus with no inner spines on dorsal face and with 4 outer spines on dorsal face.

Females not known.

SPECIMENS. *Holotype* M, PHILADELPHIA.

Tremellia beta Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Loc. 5, Mt Koghi, west slope of Mt Bouo, tall rainforest, 27 ii 1983 (Alexander, Cade, and Otte). PHILADELPHIA.

RECOGNITION. Figs. 23C, 24F, 45. Table 4. Males differ from other males in the male genitalia. Females with forewings shorter than pronotum and located on side of body (possibly nymphal?).

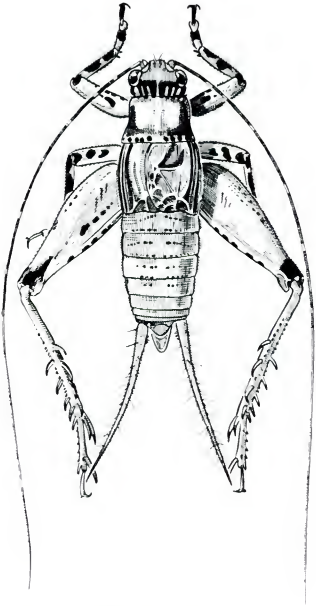


FIG. 26. *Agnotecous obscurus* male.

Males: Very similar to *alpha* but differing in male genitalia. Head: similar to *caledonica*, but stripes broader; face similar to *caledonica*. Side of forewings generally pale brown.

Females: The only female we have examined has very short forewings located on the side of the body. Because they are so small compared to those of *tiwaka* there remains the possibility that she is a nymph. Her hardened ovipositor, however, suggests that she is an adult.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratypes:* Loc. 5, 1M 1F, ANN ARBOR.

Tremellia caledonica Otte, n. sp.

TYPE. *Holotype M,* New Caledonia, Loc. 5, Mt Koghi, west side of Mt Buou, tall rainforest, 27 ii 1983 (Alexander, Cade, and Otte). PHILADELPHIA.

RECOGNITION. Figs. 22B, 23B, 24E, 45. Table 4. Distinguished from other species by the male genitalia. Head: Dorsum mostly dark brown but with 3 narrow pale longitudinal streaks. Face with broad median dark band, a pale band descending from each antennal socket and a dark band descending from each eye; cheeks blackish below eye, light brown with dark marbling below that and with a granular appearing brown band descending from lower front of eye.

SPECIMENS. *Holotype* M, PHILADELPHIA.

ENEOPTERINAE

AGNOTECOUS Saussure

TYPE SPECIES: *Agnotecous tapinopus* Saussure

RECOGNITION OF GENUS. Figs. 26-29. Table 5. Forewings of males quite unlike any other genus of Eneopterinae, the dorsal field being very small relative to the lateral field and the entire region posterior to the stridulum highly modified and abbreviated.

Males: Fig. 26. Medium to large crickets; body color reddish brown to dark brown, usually much darker on sides of body; large hindfemora; forewings not extending beyond middle of abdomen; dorsal field of forewings relatively small; hindwings absent. Head: occiput with longitudinal pale stripes, sometimes largely pale brown, with 2 to 4 dark stripes; with 3 ocelli, median ocellus located at front of rostrum; face dark brown; cheeks mostly brown or dark brown with pales areas as figured. Pronotum: dorsum widening posteriad, lighter than lateral lobes, scattered with fine dark spots; lateral lobes dark brown to black. Forewings: dorsal field very narrow relative to lateral field; mirror obsolete; chords and diagonal veins weakly to strongly modified, with one or no harp veins; lateral field with numerous parallel veins. Hindwings absent. Abdomen with fine spots often arranged in transverse rows. All tarsi with adhesive pads. Fore- and midlegs: femora reddish brown to dark brown with prominent black markings; tibiae darker than femora, with two broad black bands; foretibiae with only an outer tympanum and with 3 apical spurs; midtibiae with 4 apical spurs. Hindlegs: femora orange-brown to dark rusty brown with oblique rows of small dark spots; tibiae with 4 inner and 4 outer subapical spurs and with 3 inner and 3 outer apical spurs; inner subapical spurs longer than outer and strongly bent. Cerci medium to long, usually blotchy in color. Ovipositor laterally compressed, with serrations on dorsal margin, dorsal valves longer than ventral; with two small processes above base.

BIOLOGY. We collected *Agnotecous* on leaf litter on the forest floor; after dark many were found walking about on foliage a few feet above the ground, some on green leaves. All were found in dense wet or mesic forests both in lowlands and mountains. Although males possess a stridulum we never heard them sing. Males have a large number of file teeth in relation to the length of the stridulum, so we suspect that the sounds they make are supersonic. Conceivably the stridulatory movements transmit vibrations through the substrate.

DISTRIBITION. This genus is presently known only from New Caledonia, but related genera occur in the Solomon Islands and in Palau (Otte and Alexander in prep.).

Agnotecous obscurus (Chopard)

Lebinthus obscurus Chopard 1970: 287. *Holotype* M, New Caledonia, Col Boa, Niaouli Forest, 11 viii 1965 (Austrian Expedition). VIENNA. Type examined.

Table 5. Comparison of Agnotecous species. Abbreviations given in Methods section.

	BL	FL	OL	CL	FWL/PL	FL/TL	FL/FL	No. file teeth
obscurus								
HM	19	13.2	-	11.5	1.33	0.91	0.32	168
PM Loc.22	18.5	13.2	-	12.2	1.5	-	-	136
PF Loc.22	19	14.5	15.2	14	0.44	-	-	-
PF Loc.33	20	14.8	21.3	13.5	0.69	-	-	-
yahoue								
HM	16.5	11.2	-	10	1.33	0.85	0.36	158
PF Loc.5	16	11	10	9.0+	0.28	-	-	-
PF Loc.4	18.7	12.5	12.4	10.6	0.27	-	-	-
PF Loc.4	17.6	11.5	12	10.5	0.4	-	-	-
PF Loc.4	18	11.9	10.5	10	0.33	-	-	-
koghi								
HT	24	15.5	-	13.5	1.45	-	-	129
PM Loc.4	23	14.3	-	13.8	1.63	-	-	151

RECOGNITION. Figs. 26, 27, 29B. Table 5. Distinguished from other species by the male genitalia and the forewing venation.

Males: Dorsum of body reddish brown, side of body darker. Head: dorsum with 7 longitudinal pale streaks, one along midline, those behind eyes are broadest; face dark brown above clypeus, ivory with brown markings on clypeus and labrum; forehead pale in specimens from Loc 33 and dark in those from Loc 22. Pronotum: dorsum reddish brown with scattered darker spots; spots largest along posterior margin; lateral lobes dark brown with a pale area in lower anterior corner. Forewings dark brown. Hindwings absent. Abdomen: dorsum reddish brown, pubescent, with faint row of dark spots along posterior margins of tergites. Forelegs as in Fig. 27; midlegs similar to forelegs. Hindfemora: orange brown with numerous small dark spots on outer and upper faces and with a line of large dark spots along lower margin. Cerci dark brown.

Females: Forewings hemicircular, nearly meeting at midline (Loc 22) or slightly overlapping (Loc 33). Ovipositor of the female from Loc 22 slightly longer than findfemora; that from Loc 33 is 1.44 times as long. Possibly these two females belong to different species.

BIOLOGY. Collected in a lowland forest. Found perched on leaves a few feet above the ground.

SPECIMENS. *Holotype* M, VIENNA. *Paratypes*: (PHILADELPHIA & ANN ARBOR). Loc 16, 1F. Loc 17, 1F 1FN. Loc 22, 2M 1F 1MN. Loc 23, 1F. Loc 33, 2M 1F.

Agnotecous yahoue Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Loc. 4, Yahoué, forest along stream, 27 ii 1983 (Alexander, Cade, and Otte). PHILADELPHIA.

RECOGNITION. Figs. 28A, D, 29A. Table 5. Distinguished from other members of the genus by the male genitalia.

Males: Dorsum of body more or less unicolorous reddish brown; side of body dark brown. Head: dorsum mostly unicolorous but occiput with two short brown stripes near median and two lateral stripes; face dark brown, ivory on clypeus and labrum. Pronotum: dorsum unicol-

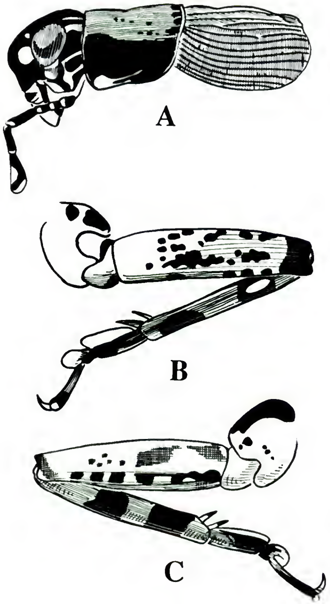


FIG. 27. *Agnotecous obscurus* . **A**, male head pronotum and forewing. **B**, foreleg (outer face). **C**, foreleg (inner face).

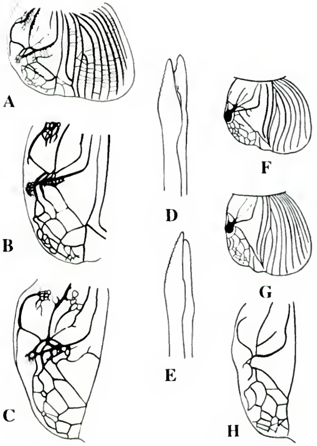


FIG. 28. *Agnotecous* forewings and ovipositors. **A**, *yahoue*. **B**, *obscurus*. **C**, *tapinopus*. **D**, *yahoue*. **E**, *obscurus*. **F**, **G**, forewings of *brachypterus* and *tapinopus* (from Gorochov 1986). **H**, *tapinopus* (from Saussure 1878).

orous; lateral lobes distinctly darker. Forewings: reddish brown, cross veins on lateral field darker than rest of wing. Abdomen: unicolorous red-brown. Fore- and midlegs: femora with some darker marking on inner and outer faces, similar in position to *amoa*, but not as contrastingly marked. Hindfemora: orange-brown with regular oblique rows of small dark spots.

Females: colored like males. Three females from Loc 4 have blackish fore- and midlegs and black sides on head and pronotum, and have 6 brown bands on vertex of head. A female from Loc 5 is much lighter in color and resembles more the holotype male. Forewings much smaller than in *obscurus*, with a wide gap seperating the left and right forewings.

BIOLOGY. We collected the members of this species mainly along oatmeal trails which we laid through the forest. It is our impression that they wander over the ground to forage. But their tarsal

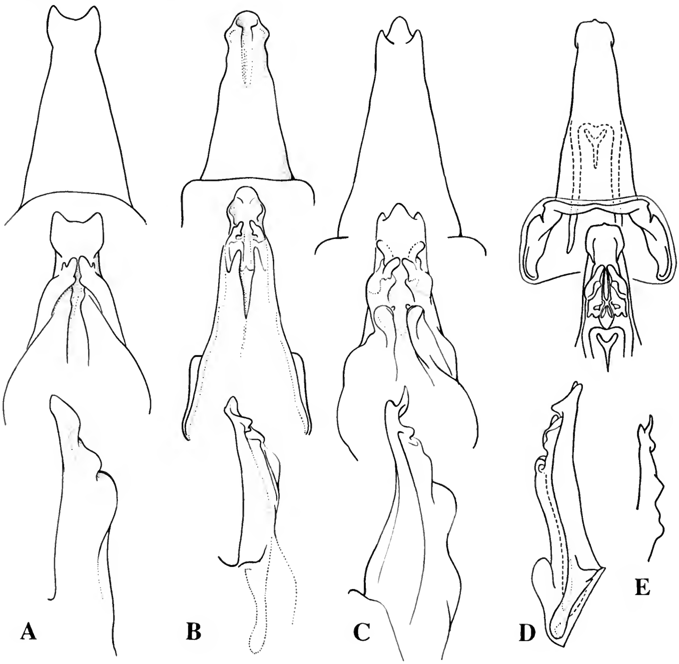


FIG. 29. *Agnotecous* male genitalia (holotypes)(from top to bottom: upper, lower and lateral views). A, *yahoue*. B, *obscurus*. C, *tapinopus*. D, *brachypterus* (from Gorochove 1986). E, *tapinopus* (from Saussure 1878).

adhesive pads suggest that they also climb onto vegetation as does *amoa*.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratypes:* (PHILADELPHIA & ANN ARBOR). Loc 4, 1M 6F. Loc 5, 1M 4F.

Agnotecous tapinopus Saussure

Agnotecous tapinopus Saussure 1878:407. *Holotype M*, New Caledonia(no other data). (Brunner de Wattenwyl, No. 5960) VIENNA. Type requested but not found, perhaps lost.

RECOGNITION. Figs. 28C, G, H, 29C, E. Table 5. Differs from other members of the genus by the male genitalia. Also considerably larger than *yahoue* and *obscurus*.

Males: Head: dorsum dark brown with 7 pale longitudinal lines, median one is very thin, lateral ones are widest; face blackish; cheeks mostly dark, with pale areas similar to *obscurus*. Pronotum: dorsum yellow brown in anterior lateral quarter, darkest in posterior third, with many small dark spots; lateral lobes black. Forewings: dorsum reddish brown; lateral field reddish brown, but veins dark brown. Fore- and midlegs: femora mostly dark brown, somewhat speckled; tibiae banded as in *obscurus*, but darker overall. Hindfemora rusty red, becoming dark brown around knees.

Females: Head dark reddish brown on dorsum, black on side of head and pronotum. Forewings slightly overlapping at midline.

BIOLOGY. We collected this species along oatmeal trails laid through tall rainforest.

SPECIMENS. Loc 4, 2M 1F; Loc 5, 1F (PHILADELPHIA & ANN ARBOR).

Agnotecous brachypterus Gorochov

Agnotecous brachypterus Gorochov 1986:701. *Holotype M*, New Caledonia (J. Bulogh)(no other data). HUNGARIAN MUSEUM. Typenot examined.

RECOGNITION. Figs. 28G, 29D. This species is readily distinguishable from other species on the basis of the male genitalia.

SPECIMEN. *Holotype* M, HUNGARIAN MUSEUM.

Agnotecous novaecaledoniae Gorochov

Agnotecous novaecaledoniae Gorochov 1986:701. *Holotype F*, New Caledonia, Mt. Rembai (J. Balogh). HUNGARIAN MUSEUM. Type not examined.

RECOGNITION. Unfortunately the type of this species is a female. It will be very difficult to separate this species from others until a male is collected.

Agnotecous robusta (Chopard) n.comb.

Eurepa robusta Chopard 1915: 149. *Holotype F*, New Caledonia, Foret du Mont Panié, alt 500 m, 27 vi 1911. BASEL.

Chopard illustrated this species profusely. It is clearly a member of Saussure's *Agnotecous*.

CARDIODACTYLUS Saussure

Chopard 1915:149 records *Cardiodactylus novae-guinea* De Haan from Oubatche. We also collected this species and it appears to be a new species which will be treated in a forthcoming revision of *Cardiodactylus*.

EUSCYRTINAE

PROTURANA Otte, n. gen.

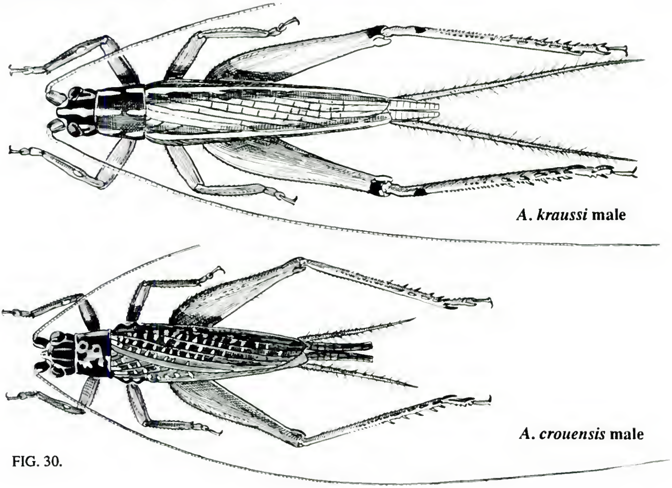
TYPE SPECIES: *Proturana subabpterus* (Chopard).

RECOGNITION OF GENUS. Foretibiae without tympana. Forewing very small, wider than long, stridulum with very tiny teeth.

Proturana subapterus (Chopard)

Euscyrtus subapterus Chopard 1970: 288. *Holotype* M, New Caledonia, Dumbea, near shore, 17 vii 1965. VIENNA. Type examined.

RECOGNITION. Figs. 20B, 22E, 25A, B. A small pale cricket with a broad dark stripe running along sides of body. Head: dorsum as figured; face entirely pale, subgnathous; cheeks pale and with a post-ocular dark band. Pronotum: dorsum as figured; lateral lobes with a dark band in upper half (dorsad this band changes gradually from pale brown to blackish). Forewings tiny, wider than long, with a stridulum. File with 209 very small teeth. Abdomen: dorsum with a faint dark central band which fades posteriorly; venter en-



A. kraussi male

A. crouensis male

FIG. 30.

tirely pale. Fore- and midfemora pale. Hindfemora with pale brown oblique markings on outer face. Cerci pale brown. Fore- and middle tibiae each with 3 apical spurs; two innermost spurs very closely spaced. Hind tibiae with 9 inner and 11-12 outer subapical spurs and with 3 inner and 3 outer apical spurs. Hind basistarsus without inner dorsal spines before apex.

HABITAT. The only male of this species was caught by sweeping through vegetation at the margin of a lowland forest on the west slope of the main range.

SPECIMENS. *Holotype* M, VIENNA. Loc 4, 1M, PHILADELPHIA.

PODOSCIRTINAE

ADENOPTERUS Chopard

Adenopterus Chopard 1951: 511. Type species: *Adenopterus norfolkensis* Chopard, by original designation.

Peltia Gorochov 1986: 704. Type species: P. roseola Gorochov 1986: 704. NEW SYNONYM.

RECOGNITION OF GENUS. Figs. 30-37. Table 6. Males: Like *Archenopterus* the members of this genus possess a gland on the forewing (forewing gland) and a very long and pointed male subgenital plate, but they differ in lacking a stridulum. In some species the forewing gland has evidently been lost secondarily, for the venation retains some similarities to that in species with well-developed glands—specifically, the R and M veins are joined near the anterior ends of the forewings. Forelegs: tympanal openings on both inner and outer faces, large and oval, nearly equal in size. Fore- and midtibiae with 2 and 3 apical spurs respectively. Hind tibiae with 5 inner and 5 outer subapical spurs and 3 inner and 3 outer apical spurs. Spurs o-1 to o-4 all small and clustered at apex.

BIOLOGY. *Adenopterus* have been collected by sweeping through low herbeage and low trees in and around forests. We have found them walking about on top of vegetation at night. Some specimens have been collected at lights, others in

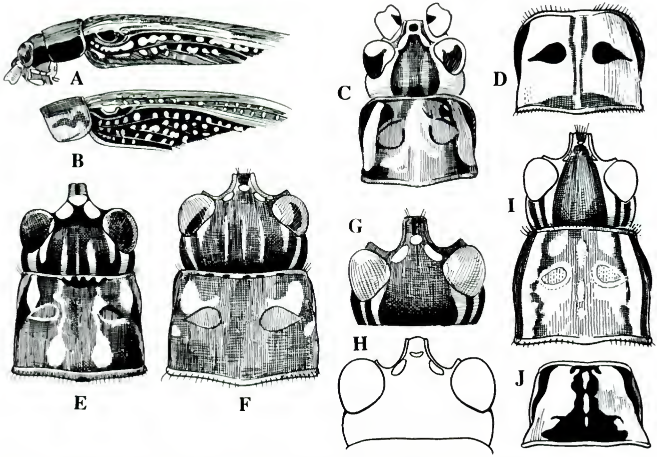


FIG. 31. *Adenopterus.* **A,** *lifouensis* male. **B,** *crouensis* male. **C,** *perplexus* . **D,** *admirandus.* **E,** *yahouensis.* **F,** *tchambicus.* **G,** *sarrameus.* **H,** *lifouensis.* **I,** *sylvaticus.* **J,** *Archenopterus bouensis* holotype pronotum.

malaise traps. Quite possibly the members of this genus are common on tree tops, but these areas have not been sampled.

DISTRIBUTION. The genus is presently known only from New Caledonia, the Loyalty Islands, and Norfolk Island.

Kraussi Group

Adenopterus kraussi Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Col des Roussettes, 300 m, 5 - 6 ii 1963, malaise trap (Yoshimoto and Krauss). HONOLULU.

RECOGNITION. Figs. 30A, 32C, 34B. Table 6. Differs from the similar *perplexus* as follows: Pronotal disc with an interrupted pale band along the lateral margins; dark streak along inner side of Cu_1 vein wide.

Males: Body mostly straw yellow, but with dark brown streaks. Head: dorsum as figured; face entirely pale; cheeks pale with dark stripe behind upper margin of eyes. Forewings: M vein only slightly modified in the forewing gland area; R vein joins M vein about one pronotal length posterior to pronotum; pale below and reddish brown above. Hindwings extending beyond ends of forewings. Abdomen straw yellow. Fore- and midlegs: femora straw yellow with a few scattered darker spots. Hindfemora: straw yellow with a few small darker spots; knees black on upper face and on crescents.

Female: very similar to male but larger. Females from Mt Panié and Col d'Amieu have relatively longer ovipositors.

SPECIMENS. *Holotype* M, HONOLULU. *Paratypes*: Same data as type, 1F, HONOLULU. Mt Panié, forest, 500 m, 27-29 vii 1971 (Gressitt) 1F, HONOLULU. Col d'Amieu, 650 m, 21 iii 1968 (Gressitt and Maa) 1F, PHILADELPHIA.

Adenopterus sylvaticus Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Mt. Koghi, west slope of Mt Bouo, ii 1983 (Alexander, Cade, and Otte). PHILADELPHIA.

RECOGNITION. Figs. 31I, 32F, 33K, L, 34A. Table 6. Differs from the similar *euperplexus*

Table 6. Comparison of Adenopterus species. See Methods section for abbreviations. V, number of parallel longitudinal veins on dorsal surface of forewings, other than Cu1.

	BL	FL	OL	CL	FWL/PL	OL/FL	V
kraussi							
HM	17	9.3	-	8.0+	4.9		7
PF Amieu	15	10.5	9		5	0.86	
PF Yahoue	16	10.1	7.2	10	-	0.71	10
PF Panie	16	10.2	8.8	11.5	5.3	0.86	9
sylvaticus							
HM	15	8	-	11	4.15	-	6
PM	14	8.2	-	-	5.27	-	6
sarasini							
HM	14.5	-	-	-	3.77	-	6
PF Amieu	13	9	7.2	-	4.17	0.85	
PF Panie	12	8.3	7	8+	3.53	0.84	6
rouxi							
HM	12	-	-	-	3.9	-	6
caledonicus							
HM	14	7	7	-	6.3	0.92	7
dumbeus							
HM	-	8.54	7	-	4.8	0.83	7
PF	13.5	9	7.5	10.5	4.3	0.83	7
confixus							
HT	14	9.5	8.5	-	6	0.89	8
dubius							
HT	20	13	16	18	5.5	1.23	7
perplexus							
HT	17	10	7	-	6.2	0.7	10
PF Yahoue	13	9.5	7.3	-	6.2	0.77	9
PF Yahoue	15	9.8	7.2	-	6.3	0.73	9
PF Koghi	17	10.5	7.3	-	6.4	0.7	9
PF Koghi	15	10.5	7.2	10	6.3	0.69	10
paraperplexus							
HT	14	9	7.3	9	6.7	0.81	11
euperplexus							
HT	11	8.1	7	9.9	6.9	0.86	9
PF	13	8.8	7.1	8.5	6.4	0.81	9
sarrameus							
HT	15	9.5	-	-	4.8 -	8	
PF	14-17	10.0-11.2	13.5-15.5	-	4.4-4.7	1.3-1.4	8-9
yahouensis							
HM	12	8.3	-	-	4.8	-	7
9PF Yahoue	14-17	10.0-11.0	12.8-15.0	12.0-13.5	4.3-4.7	1.28-1.36	8-9
3PF Thy	14-16	10	13	-	-	-	8
1PF Pines	16	10.1	13.2	11	4.1	1.31	8
tchambicus							
HM	13	9	-	6.0+	4.6	-	8
admirandus							
HM	17	11.3	17	18	4.4	1.5	10
4PF Mt Koghi	15-17	11.0-11.5	17.0-18.0	17.0-18.0	4.3-4.8	1.48-1.6	9-10

Table 6 (continued)

	BL	FL	OL	CL	FWL/PL	OL/FL	V
crouensis							
HM	12	7.8	-	8	5.7	-	7
2PM Timbia	11, 10	6.8,6.7	-	6.0,5.5	6.3,5.5	-	6, 7
PM Noumea	10	7.8	-	-	6.1		6
PM La Crouen	11	7.7	-	-	5.7	-	7
2PM Yahoue	10, 12	6.5,7.0	-	6.0,7.0	5.5,6.0	-	6, 7
PF Timbia	12	9	11	11	5.9	1.22	7
PF Noumea	13	8	10	10	5.7	1.25	6
PF Thy	14	8.7	10.5	-	5.6	1.21	7
PF La Crouen	13	9	11.2	-	5.4	1.24	6
PF Dumbea	11	8	9.5	-	5.8	1.19	7
PF La Coulee	14	9	10	-	5	1.11	7
lifouensis							
HM	12	6.5	-	-	5.4	-	5
PM	11	6.5	-	-	-	-	
PF	12	8.2	8.2	-	-	1	6
noumeus							
HM	11	7	-	6.2	5.4	-	6
4PF	12-11.3	7.2-8.5	8.2-9.0	8.5-9.0	5.2-5.5	1.09-1.14	6-7

and *paraperplexus* in having only 6-7 dorsal paralled veins on the forewings (vs 9-11). Last abdominal tergite modified into a large plate which extends over the bases of the cerci.

Males: Body color uniform pale orange-brown. Head: dorsum pale brown, banded with darker stripes; area between eyes and ocelli may be dark brown. Face light brown at top of forehead, otherwise ivory colored; cheeks ivory, but with 2 brown stripes emerging from posterior margin of eye. Pronotum patterned as figured; lateral lobes light brown. Forewings: forewing gland similar to that of *kraussi*; dorsal field straw colored to orange-brown, with slightly reddish veins; with a few cross veins; lateral field orange brown above, becoming yellowish ventrad. Hindwings extending about one pronotal length beyond forewings. Abdomen: dorsum pale brown; Fore- and midlegs: ivory with small brown spots on upper face. Hindfemora pale, with a single longitudinal row of spots on upper face, and with numerous pale brown oblique stripes on outer face; knees with black crescents. Cerci pale with 4 - 5 short dark crossbands.

Females: Similar to males. On the forewings the R vein (which does not join the M vein) defines the forewing angle. Last tergite of abdomen not modified as in male.

SPECIMENS. *Holotype* M, PHILADELPHIA. *Paratypes*: Mt Koghi, 400 - 600 m, i 1969 (Krauss) 1M, HONOLULU.

Adenopterus sarasini (Chopard)

Podoscirtus sarasini Chopard 1915: 160. Holotype M, New Caledonia, Canala, 1911 (Dr. S. R.). BASEL. *Munda sarasini*, Chopard 1968: 412. NEW COMBINATION. Type examined.

RECOGNITION. Figs. 33F, 35B. Table 6. Very similar to *sylvaticus* but differing in having shorter ectoparameres, and in the venation associated with the wing gland (see figures). Differs

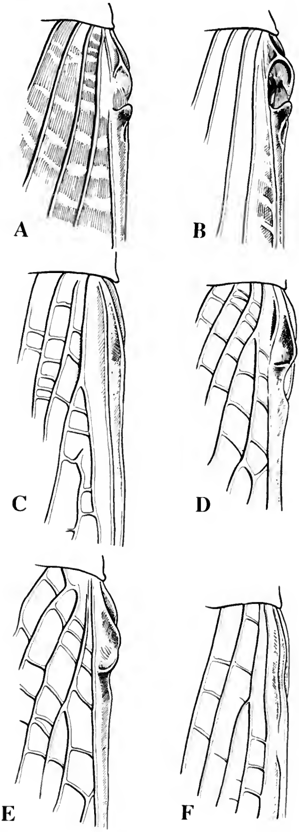


FIG. 32. *Adenopterus* male forewing showing forewing gland or traces of the gland. A, *crouensis* B, *lifouensis*. C, *kraussi*. D, *tchamicus*. E, *yahouensis*. F, *silvaticus*.

from *caledonicus* in the shape of the male epiphallus.

SPECIMENS. *Holotype* M, BASEL. *Paratypes*: Col d'Amieu, 750 m, 3 iii 1960 (Gressitt) 1F, HONOLULU. West of Ponerihouen, 29 vii 1971 (Gressitt) 1F, PHILADELPHIA. Mt Panie, 700 m, 27 vii 1971 (Gressitt) 1F, HONOLULU.

Adenopterus rouxi (Chopard)

Podoscirtus rouxi Chopard 1915: 160. *Holotype* M, New Caledonia, Mt. Panié, 1400 m, 28 vi 1911 (Dr. S. R.). BASEL. *Munda rouxi*, Chopard 1968: 412. NEW COMBINATION. Type examined.

RECOGNITION. Figs. 33C, 35A. Table 6. Differs from *sylvaticus*, *sarasini*, and *caledonicus* in the shape of the male genitalia and the venation of the forewings (see figures).

SPECIMENS. *Holotype* M, BASEL.

Adenopterus roseola Gorochov, n. comb.

Peltia roseola Gorochov 1986:704. *Holotype M*, New Caledonia, Noumea (J. Bulogh). HUNGARIAN MUSEUM. NEW COMBINATION. Type not examined.

RECOGNITION. Fig. 34C.

Adenopterus caledonicus Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Yahoue, west slope of Mt. Bouo, 26 ii 1983 (Alexander, Cade & Otte). ANN ARBOR.

RECOGNITION. Figs.36C. Table 6. Males with no trace of forewing gland.

Male: Body color yellowish with ivory legs. Head: dorsum uniformly yellowish with large ocelli; face and cheeks ivory. Pronotum: dorsum yellowish with two ivory pale longitudinal pale marks along each lateral margin; lateral lobes ivory in lower two-thirds, orange in upper third

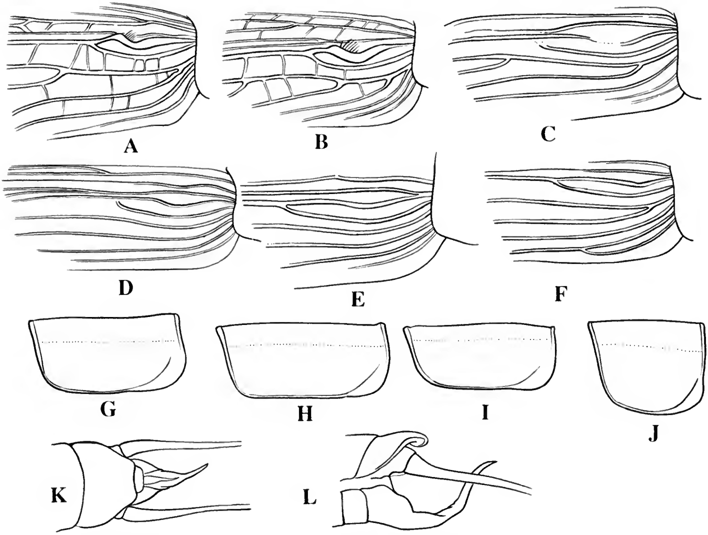


FIG. 33. *Adenopterus*. A-F, lateral aspect of forewing showing venation associated with forewing gland. A, *sarrameus*. B, *yahouensis*. C, *rouxi*. E, *sylvaticus*. F, *sarasini*. G-J, lateral aspect of pronotum. G, *sylvaticus*. H, *sarasini*. I, *rouxi*. J, *euperplexus*. K,L, dorsal and lateral aspects of male *sylvaticus* showing development of the last abdominal tergite and the elongate subgenital plate.

and with two longitudinal pale patches along upper margin. Forewings: without any trace of a forewing gland; membrane yellow to ivory, veins all reddish brown; with 7 longitudinal veins; lateral field yellowish with brownish veins. Hindwings: extending about one pronotal length beyond forewings. Abdomen: ivory colored, but last sternite before subgenital plate with a small dark brown mark on each side. Foretibiae with a brown area on upper face between the tympana. Legs all ivory colored. Hind tibiae with a small black area at base of each spur.

HABITAT. Collected in foliage at the forest edge by sweeping.

SPECIMENS. *Holotype* M, ANN ARBOR.

Adenopterus dumbeus Otte, n. sp.

TYPE. *Holotype* F, New Caledonia, Dumbea, Uferregion [coastal region] 12 viii 1965 (Östereichische Neukaledonien Expedition, 1965). VIENNA.

RECOGNITION. Table 6. Forelegs without tympana (this feature is unique for crickets which are capable of flight).

Females: Unlike all other *Adenopterus* or *Archenopterus* species this species lacks any trace of tympana. This is a highly unusual condition, for no other species of cricket that possesses flying hindwings lacks tympana. This feature could have arisen if both front legs were

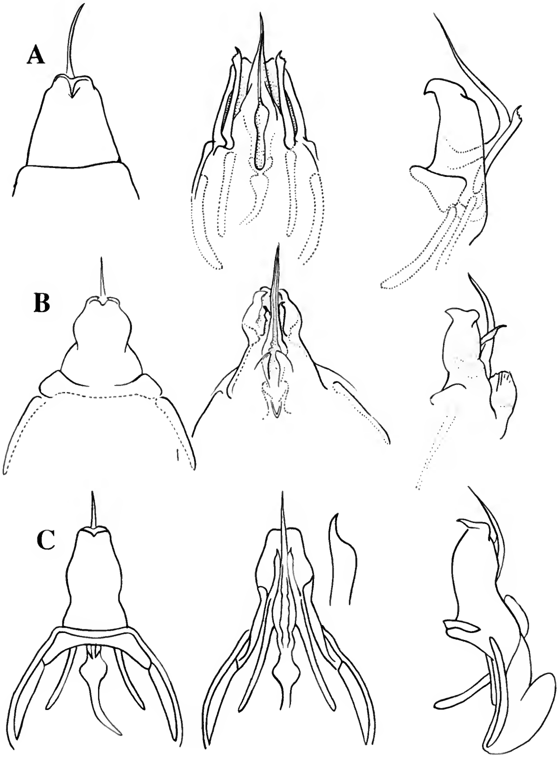


FIG. 34. *Adenopterus* male genitalia (holotypes). A, *sylvaticus*. B, *kraussi*. C, *roseola* (from Gorochov 1986).

7

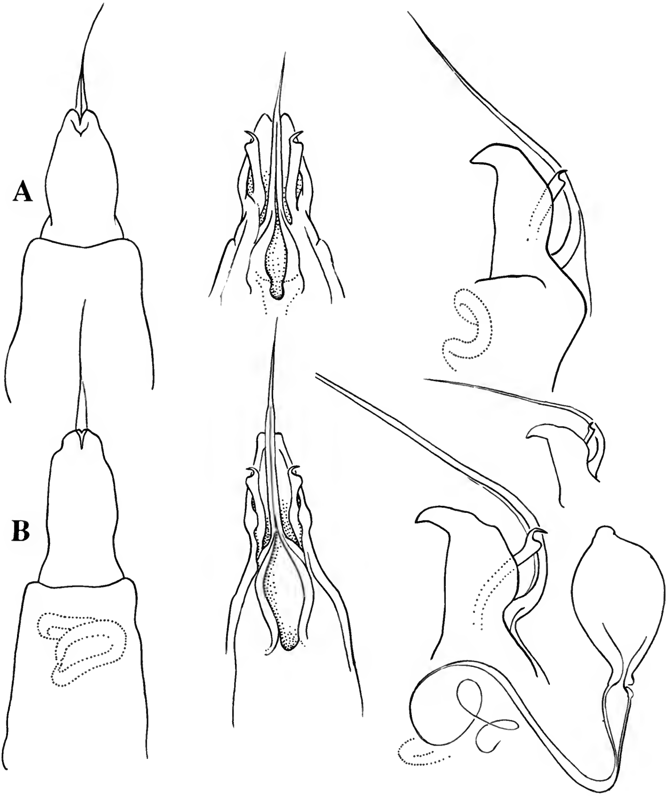


FIG. 35. *Adenopterus* male genitalia (holotypes). A, *rouxi*. B, *sarasini*.

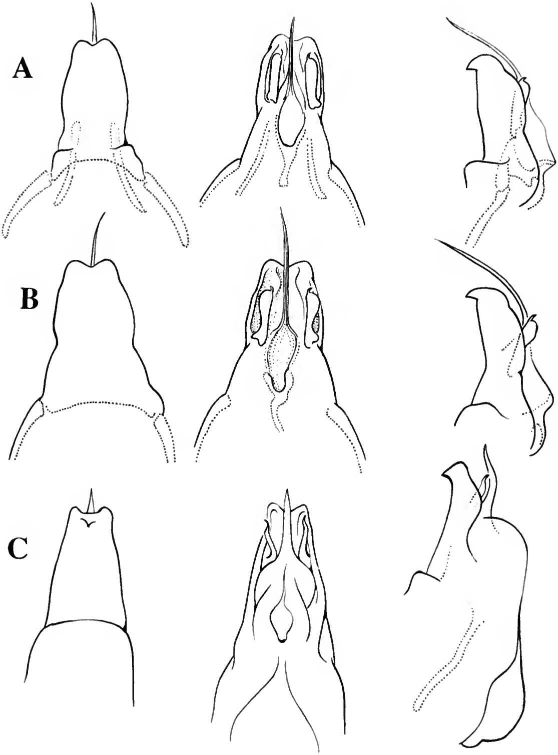


FIG. 36. *Adenopterus* male genitalia (holotypes). A, *yahouensis*. B, *sarrameus*. C, *caledonicus*.

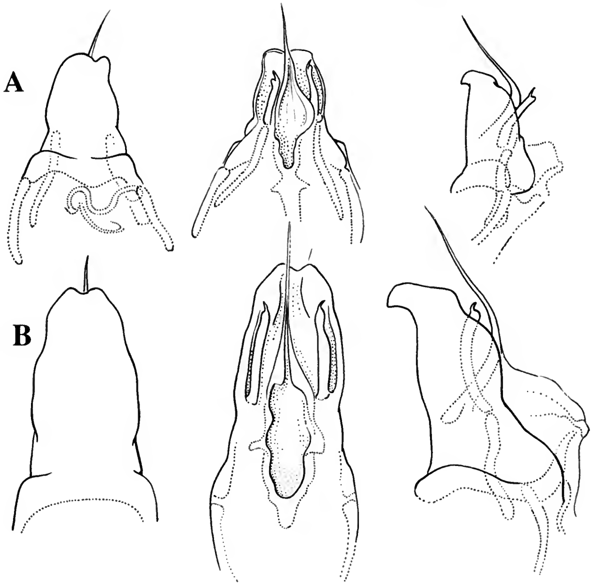


FIG. 37. *Adenopterus* male genitalia (holotypes). A, *crouensis*. B, *lifouensis*.

lost during nymphal stages and were regenerated. Because of the close similarity between females of *Adenopterus* and *Archenopterus* there is some doubt as to which genus this female belongs to. We place it here because *Archenopterus* males still possess stridula while males of *Adenopterus* do not. It seems more likely therefore for the latter to more readily lose their tympana.

Body color dark reddish brown, almost purple (but forewings grayish) and without any pale markings. Head: entirely dark reddish brown except for labrum which is yellow; with 3 small ocelli. Pronotum entirely dark reddish brown. Forewings gray with dark veins; dorsal field with 7 parallel veins (not including Cu_1). Hindwings extending about 1.5 pronotal lengths beyond forewings. Legs all dark reddish brown. Hind tibiae with 5 inner and 6 outher subapical spurs.

Males: not known.

SPECIMENS. *Holotype* F VIENNA. *Paratype*: New Caledonia, Mt. Mou, 3 ii 1963 (Krauss) HONOLULU.

Adenopterus confixus Otte, n. sp.

TYPE. *Holotype* F, New Caledonia, Plateau do Dogny, 29 iii 1968 (Gressitt and Maa). HONOLULU.

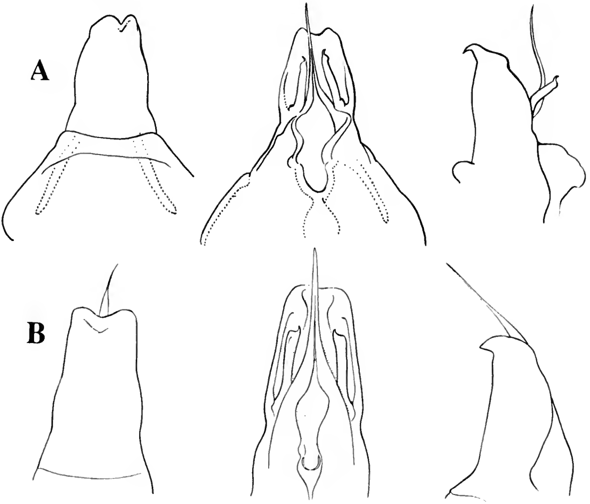


FIG. 38. *Adenopterus* male genitalia (holotypes). A, *saussurei*. B, *tchambicus*.

RECOGNITION. Table 6. Cu_1 vein dark brown in anterior half of forewings; hind knees black (in *sylvaticus*, *euperplexus* and *paraperplexus* Cu_1 veins is pale brown or yellow, and the hind knees are not black).

Females: Body color pale brown but with dark brown pronotum and head; dorsal field of forewings with a thin dark brown streak along each side. Head: Dorsum dark brown, lateral ocelli huge, meeting at midline; median ocellus very small; face yellow; cheeks yellowish below, turning rusty-red dorsad. Pronotum: dorsum dark reddish brown, darkest in anterior lateral quarters, MAPs paler than surrounding areas, lateral lobes dark reddish-brown in upper two thirds, yellowish in ventral third. Forewings: pale brown, but with dark streaks along lateral margins (along R, M, and Cu1 veins, anteriorly the dark streak runs between and includes the Cu_1 and Cu_2 veins; the Cu_2 vein itself is the darkest portion, but it is dark only in the basal half of the wing; lateral field pale brown. Hindwings extend about 1.5 pronotal lengths beyond the forewings. Abdomen: dorsum pale reddish brown, venter yellowish. Fore- and midlegs: pale brown; tibiae with a large black dorsal spot in the proximal third—on the foretibiae the spot is located at the upper end of the tympanum. Foretibiae with 2 and middle tibiae with 3 apical spurs. Hindfemora very pale, but knees black; hind tibiae with 5 dark brown spots located along the posterior margin between the spines — 3 in the proximal half and 2 in the distal half; with 5 inner and 5 outer subapical spurs.

Males: not known.

SPECIMENS. *Holotype* M, HONOLULU.

Adenopterus dubius Otte, n. sp.

TYPE. *Holotype* F, New Caledonia, Col de Rousettes, 6 ii 1963 (Krauss). HONOLULU.

RECOGNITION. Table 6. Forewings with R, M, and Cu_1 veins blackish through most of their length.

Females: Body color gray, dark brown, and black, with brown Hindfemora. Head: dorsum dark brown to blackish, lighter posterior to eyes; lateral ocelli large, median one very small. Pronotum: dorsum and lateral lobes dark brown to blackish. Forewings: mostly gray, but pale brown at anterior lateral corners and along pronotal margin, black along forewing angle (R, M, and Cu_1 are yellowish at their base and then turn black for the remainder of their lengths. Vein Cu_2 black at the base then turning yellowish or pale brown as it enters gray area of the forewing. Hindwings black as they emerge from the forewings. Abdomen: brown to dark brown. Fore- and midlegs: femora brown to reddish-brown, midfemora with a broad black streak on the inner face. Hindfemora: pale brown with black knee crescents.

Males: Not known.

SPECIMENS. *Holotype* F, HONOLULU.

Adenopterus perplexus Otte, n. sp.

TYPE. *Holotype* F, New Caledonia, Mt Koghis, 400 - 600 m, i 1969 (Krauss). HONOLULU.

RECOGNITION. Fig. 31C. Table 6. Most similar to *sylvaticus* but larger and more contrastingly marked, especially in the vicinity of the ocelli, and forewings with distinct pale and dark veins at the lateral edge of the dorsal field.

Females: Head: In some specimens MAPs darker than surrounding area; face and cheeks yellowish. Pronotum: dorsum marked as in Fig. and with continuous lateral yellow bands; lateral lobes dark reddish brown in lower three-quarters and yellow across the dorsal quarter. Forewings: with a narrow dark brown streak running along inner side of Cu_1 vein; veins variable in color — Sc pale, Sc branches brownish; R dark brown; M thick and yellow in basal half, turning pale brown in distal half; Cu_1 brownish in basal quarter, yellow in remainder; Cu_2 brown, somewhat sinuous. Hindwings extending 2 pronotal lengths beyond forewings. Fore- and midlegs pale brown with dark brown area on inner and outer faces; tibiae pale brown but darker brown on upper face through most of the central portion. Hindfemora yellowish, sometimes with small black spots on outer face.

Males: not known.

SPECIMENS. *Holotype* F, HONOLULU. *Paratypes*: (HONOLULU) Mt Koghis, 25 i 1962 (Krauss) 1F. ii 1963 (Krauss) 1F. ii 1973 (Krauss) 1F. Yahoue, 20 ii 1963 (Yoshimoto) 1F. Yahou, i 1963 (Krauss) 1F.

Adenopterus paraperplexus Otte, n. sp.

TYPE. *Holotype* F, New Caledonia, Plateau do Dogny, 29 iii 1968 (Gressitt). HONOLULU.

RECOGNITION. Table 6. Similar to *perplexus* but differs as follows: dorsum of head not banded; with a shallow transverse groove running between eyes and posterior to lateral ocelli (in *perplexus* the head slopes continuously and gradually from the vertex onto the rostrum); Sc vein darker than R vein; R and M veins similar in color (pale brown); dorsal field with 11 parallel veins (9 - 10 in *perplexus*); dorsal field without a brown streak running along the inners side of the Cu_1 veins; ovipositor relatively longer.

Females: Body color pale brown.

Males: not known.

SPECIMENS. *Holotype* F, HONOLULU.

Adenopterus euperplexus Otte, n. sp.

TYPE. *Holotype* F, Baie du Prony, west side, 0 - 10 m, 14 viii 1979 (Gagne). HONOLULU.

RECOGNITION. Fig. 33J. Table 6. Very similar to *perplexus* and *paraperplexus*. Differs from *perplexus* in body proportions (body smaller, forwings and ovipositor relatively longer), and coloration (lateral lobes of pronotum not pale brown; Sc vein darker than R vein; dorsal field of forewings without a dark streak along the inner side of the Cu_1 vein). Differs from *paraperplexus* in having 9 parallel veins on dorsal field of forewings; in lacking the pronounced shallow groove which runs transversely between the eyes. Hindwing extends 1.5 - 2 pronotal lengths beyond the forewings. Body color pale brown.

Males: not known.

SPECIMENS. *Holotype* F, HONOLULU. *Paratypes*: Yate, 25 iii 1968 (Gressitt and Maa) 1F, HONOLULU. Poindimie, 11 ii 1963 (Krauss) 1F, HONOLULU.

Sarrameus Group

Adenopterus sarrameus Otte, n. sp.

TYPE. *Holotype* M, New Caledonia, Sarramea, 70-150 m, ii 1971 (Krauss). HONOLULU.

RECOGNITION. Figs. 31G, 33A, 36B. Table 6. Very similar to *yahouensis*, but with smaller ocelli, and different genitalia.

Males: Head: dorsum reddish brown; face dark reddish brown above clypeus, ivory on clypeus and labrum; cheeks reddish brown with a yellowish spot along lower margin of eye. Pronotum: like *yahouensis*. Forewings: dorsum gray with dark reddish veins, yellow anterior to glandular area. Hindwings extending one pronotal length beyond forewings. Abdomen: 9th tergite black; venter yellowish, black at base of subgenital plate. Legs: similar to *yahouensis*.

Females: similar to males in color. Largely indistinguishable from *yahouensis*.

SPECIMENS. *Holotype* M, HONOLULU. *Paratypes*: Sarramea, ii 1971 (Krauss) 1M 1F, PHILADELPHIA; 3F, HONOLULU. La Crouen, 12 iii 1961 (Sedlacek) 1F, HONOLULU. Col d'Amieu, 650 m 31 iii 1968 (Gressitt) 2F, HONOLULU.

Adenopterus yahouensis Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Yahoué, iii 1978 (Krauss). HONOLULU.

RECOGNITION. Figs. 32E, 33B, 36A. Table 6. Very similar to *sarrameus*, but with huge ocelli.

Males: Head, thorax and legs reddish, forewings gray, but white at anterior-lateral shoulders. Head: dorsum reddish-brown, ocelli extremely large, lateral ones touching median one; face brown above clypeus, ivory on clypeus and labrum, palps ivory; cheeks reddish brown with a yellow area along lower posterior margin of eye. Pronotum: lateral lobes reddish brown, darker in upper half. Forewings: membrane gray, with dark reddish veins, yellow at anterior lateral shoulders. Fore- and midlegs: femora dark reddish-brown on inner and outer faces, ivory with dark spots on upper face; tibiae dark reddish brown. Hindfemora: dark markings on dorsal face joining into 3 brownish bands, knees also dark, outer face with a brown band below middle, ivory along dividing line, with rows of dark spots above line and brown blotches above that.

Female: Very similar to males.

SPECIMENS. *Holotype* M, HONOLULU. *Paratypes*: Yahoue, 11 1980 (Krauss) 1M, HONOLULU; 1M, PHILADELPHIA. Yahoue, 12 ii 1962, i 1963, 2 iii 1976 (Krauss) 9F, HONOLULU; 1F, PHILADELPHIA. 6 km north of Païta, 25 i 1963 (Yoshimoto) 1F, HONOLULU. Foret de Thi, 100 - 200 m, 10 iii 1961 (Sedlacek) 2F, HONOLULU. Foret de Thy, 550 m, 1 iii (Sedlacek) 1F, HONOLULU. Isle of Pines, iii 1959 (Krauss) 1F, HONOLULU.

Adenopterus tchambicus Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Tchamba River, east of Tchamba, near Ponérihouen, 3 iii 1983 (Alexander, Cade, and Otte). PHILADELPHIA.

RECOGNITION. Figs. 31F, 32D, 38B. Table 6. Head and pronotal patterns similar to *yahouensis* but as dark, and ocelli much smaller, more like *sarrameus*.

Males: Very similar to *sarrameus* and *yahouensis*. Forewing glands similar to *sarrameus*. Hindwings extend one pronotal length beyond forewings. Abdomen: dorsum dark brown on last two tergites; venter yellow, black at base of subgenital plate

Females: not known.

BIOLOGY. Collected in a hillside forest by sweeping through the underbrush.

SPECIMENS. *Holotype* M, PHILADELPHIA.

Adenopterus admirandus Otte, n. sp.

TYPE. *Holotype F*, New Caledonia, Foret de Thy, 550 m, 1 iii 1960 (Gressitt). HONOLULU.

RECOGNITION. Fig. 31D. Table 6. Body color pale yellowish brown with a dark brown head and with two darp brown patches on the yellowish pronotal disc.

Females: Head: dorsum dark brown with a pale stripe running from posterior inner margin of the eye to pronotum and with yellowish bands running from inner front margins of eyes through lateral ocelli and along lateral margins of rostrum. Rostrum with a median dark brown stripe (widest just anterior to median ocellus) and interrupted at median ocellus, but continuing posteriorly to Y-shaped suture located between the lateral ocelli; exterior margins of rostrum dark brown. Pronotum: dorsum yellowish, with dark brown MAPs; lateral lobes mostly dark reddish brown, palest along anterior and posterior margins. Forewings pale brown with yellowish veins. Hindwings dark brown, extending 0.5 pronotal lengths beyond forewings. Fore- and midlegs reddish brown. Hindfemora pale brown in basal half, turning reddish brown in distal half, knees yellow; hind tibiae reddish brown. Cerci reddish brown.

Males: Not known.

SPECIMENS. *Holotype* F, HONOLULU. *Paratypes*: Mt. Koghi, i 1963 (Krauss) 1F, HONOLULU; 15 ii 1963 (Yoshimoto) 1F, HONOLULU; ii 1963 (Krauss) 1F, PHILADELPHIA; i 1969 (Krauss) 1F, HONOLULU.

Crouensis Group

Adenopterus crouensis Otte, n. sp.

TYPE. *Holotype* M, New Caledonia, La Crouen, 150 - 250 m, ii 1973 (Krauss). HONOLULU.

A member of Saussure's type series of *Podoscirtus insularis* from New Caledonia belongs to this species. That specimen, numbered 4734, was designated as a variety by Saussure 1878: 640.

RECOGNITION. Figs. 32A, 37A. Table 6. Body color dark reddish brown to purple, with rows of white spots on forewings; with a row of white spots between all veins. The similar *A. lifouensis* lacks white spots between the central veins.

Males: Head: dorsum dark reddish brown, shiny, size of ocelli similar to *sarrameus;* face and cheeks shiny black. Pronotum: entirly dark reddish brown with long silvery pubescence. Forewings: gland large and deep; membrane gray, veins dark reddish brown, cross veins white and oval. Hindwings extending nearly 2 pronotal lengths beyond forewings. Legs reddish brown.

SPECIMENS. *Holotype* M, HONOLULU. *Paratypes*: *Syntype* F of *Podoscirtus insularis* Saussure, New Caledonia (Brunner Collection No. 4734) VIENNA. Yahoue, iii 1978 (Krauss) 1M, HONOLULU; 1M, PHILADELPHIA. Oua Tom, 20 ix 1940 (FXW) 1M, HONOLULU. 2 km SE of Timbia, Ngoue 0 - 5 m, 20 ix 1979 (Gagne) 2M 2F, HONOLULU. Noumea, 1 1962 (Krauss) 1F, HONOLULU; vii 1950 (Krauss) 1M, HONOLULU. Foret de Thi, 100 - 200 m, 10 iii 1961 (Sedlacek) 1F, HONOLULU. La Crouen, 31 i 1963 (Yoshimoto & Krauss) 1M, HONOLULU; 20 iii 1968 (Gressitt & Maa) 1F, PHILADELPHIA. Dumbea Valley, vi 1950 (Krauss) 1F, HONOLULU. La Coulee, 23 i 1963 (Yoshimoto) 1F, HONOLULU. La Foa, 20 i 1945 (Milliron) 1F, HONOLULU.

Adenopterus lifouensis Otte, n. sp.

TYPE. *Holotype M*, Loyalty Islands, We, Lifou Island, 16 - 18 ii 1963 (Yoshimoto). HONOLULU.

RECOGNITION. Figs. 31H, 32B, 37B. Table 6.

A dark reddish brown species with white spots mainly along the sides of the forewings.

Males: Head: dorsum dark brown, with large yellow ocelli; face and cheeks reddish brown. Pronotum: dorsum dark brown with long golden pubescence; lateral lobes black in lower half. Forewings: gland large and deep; dorsum brown centrally and with a wavy white band along the margins; lateral field with rows of white spots. Legs uniformly reddish brown. Hindlegs: femora brown, tibiae darker than femora.

SPECIMENS. *Holotype* M, HONOLULU. *Paratypes*: Same data as holotype, 1M, PHILADELPHIA. Same locality but ii 1962 (Krauss) 1F, HONOLULU. Lifou Island, 1 km W of Doueoulou, 5 - 35 m, 19 viii 1979 (Gagne) 1F, HONOLULU.

Adenopterus saussurei Chopard

RECOGNITION. Fig. 38A. Table 6. Nearly identical to *lifouensis*, but differing in the shape of the male epiphallus. Forewing glandular pits similar to *lifouensis*. We treat these specimens as distinct from *lifouensis* because more than 100 km of water separates them and differences exist in the epiphalli (more pointed in *noumeus*).

Females: very similar to females of *lifouensis*.

SPECIMENS. New Caledonia, Noumea, light trap, 20 ii 1963 (Yoshimoto & Krauss). 1M, 4F, HONOLULU & PHILADELPHIA.

Adenopterus baloghi Gorochov

Adenopterus baloghi Gorochov 1986:706. Isle of Pines, New Caledonia, 10 i 1977 (J. Balogh). HUNGARIAN MUSEUM. Type not examined.

The type is a female from the Isle of Pines.

ARCHENOPTERUS n. gen.

TYPE SPECIES: *Archenopterus gressitti* Otte, n. sp.

RECOGNITION OF GENUS. Figs. 39-44. Table 7. Medium sized for subfamily: BL 13 - 19 mm. Forewings with a stridulum, also with a forewing gland at anterior end of M vein (size and depth of organ varies among species). Head: with 3 ocelli, median one usually smaller than lateral ones, in one species very tiny. Maxillary palps with a short, wide, ultimate segment. Pronotum widening strongly posteriorly in species with wide forewings. Inner chord connecting to diagonal vein and not to outer two chords. Harp with 5 - 10 veins. Sc vein with 6-10 branches. Hindwings extending beyond forewings. Subgenital plate elongate and pointed at apex (as in *Adenopterus*). Foretibiae with both inner and outer tympana, these are large and nearly equal in size. Foretibiae with 2 and midtibiae with 3 apical spurs. FW/FL, 0.20 - 0.27. Hindtibiae with 5 inner and 5 outer apical spurs (all located in distal half) and with 3 inner and 3 outer apical spurs. Spurs o-1 to o-4 small, closely spaced at apex. Cerci long and slender.

Archenopterus gressitti Otte, n. sp.

TYPE. *Holotype* M, New Caledonia, Mt Koghi, 28 viii 1968 (Gressitt and Maa). HONOLULU.

RECOGNITION. Figs. 39B, 40A, 41B, 42A. Table 7. *Males*: Body color pale brown, forewing glands large and deep. Head: median ocellus distinctly smaller than lateral ones; vertex and occiput pale brown, becoming dark brown on forehead between ocelli; face and cheeks pale brown. Pronotum: entirely pale brown. Forewings: dorsum pale brown, covered with fine pubescence; Sc with 8 branches. Hindwings: extenting 2 pronotal lengths beyond forewings. Legs all uniformly pale brown.

Females: not known.

Table 7. Comparison of Archenopterus species.

	BL	FL	OL	CL	FWL/ PL	TL/ FL	No. file teeth
hemipteroides							
HM	19	11	-	-	5.1	0.9	230
PF Rousettes	19	13	11.5	-	5.4	0.91	-
PF Amieu	17	12.3	11	16	5.8	-	-
bouensis							
HM	20	12	-	-	5.4	0.92	298
gressitti							
HM	17	11.1	-	-	5	0.92	209
amoensis							
HM	13.3	7.7	-	15	5.7	0.96	-
maai							
HM	13.5	8.5	-	8	6	0.99	220
hemiphonus							
HM	12	8.5	-	-	5.8	-	28

SPECIMENS. *Holotype* M, HONOLULU.

Archenopterus maai Otte, n. sp.

TYPE. *Holotype* M, New Caledonia, Mt Koghi, 18 viii 1968 (Gressitt and Maa). HONOLULU.

RECOGNITION. Figs. 39C, 40E, 41C, 43A. Table 7. *Males*: Dorsum of body patterned as figured. Head: dorsum with a single broad band behind each eye, and with a yellow stripe running from inner margin of eye through the lateral ocelli and onto forehead; face straw yellow, but with two small dark stripes descending from dorsum onto upper face; cheeks mostly reddish brown posterior to eyes, yellowish below eyes. Pronotum: dorsum reddish brown with lateral yellow stripes; lateral lobes pale brown. Forewings: dorsum gray with dark brown veins, with a narrow ivory stripe along forewing angle; lateral field pale brown, dark brown between Sc and R veins and along forewing glands. Hindwings extending about 3 pronotal lengths beyond forewings. Fore- and midlegs pale reddish brown. Hindfemora pale brown with rows of scattered spots along its length. Cerci pale.

Females: Not known.

SPECIMENS. *Holotype* M, HONOLULU. *Paratypes*: Yahoue, 60 - 100 m, ii 1980 (Krauss) 1M, PHILADELPHIA. Mt. Koghis, 400 - 600 m, i 1969 (Krauss) IM, HONOLULU.

Archadenopterus hemipteroides Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Mt Panie, 500 - 1000 m, 11 x 1967 (Sedlacek). HONOLULU.

RECOGNITION. Figs. 39A, 40B, 41A, 42B. Table 7. Males with broad shoulders on forewings, pronotum widening strongly posteriorly, and with a narrow head.

Males: Blackish on shoulders of forewing, sides of pronotum and top of head. Head: dorsum dark brown becoming black cephalad between ocelli and rostrum, lateral ocelli large, median ocellus small, almost obsolete; face and cheeks straw yellow. Pronotum: dorsum mostly pale reddish brown, turning black at margins; lateral

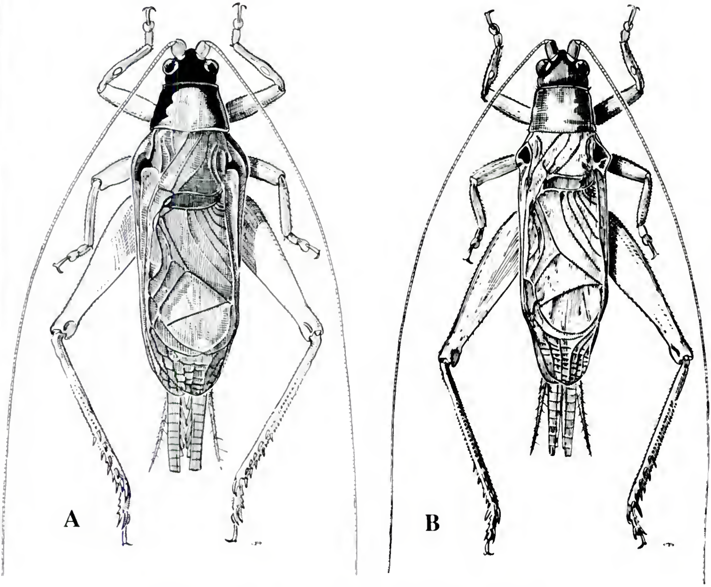


FIG. 39. *Archenopterus*. **A**, *hemipteroides* male. **B**, *gressitti* male.

lobes black in upper two thirds, pale along lower margin. Forewings: dorsum with huge forewing glands, very broad, pale brown on most of dorsal surface, dark brown to black anterior to glands; lateral field with 9 branches of Sc vein. Hindwings extending 1.5 pronotal lengths beyond forewings. All femora and cerci uniformly pale brown.

Females: body much narrower than in males, especially through the forewings. Body color pale brown, but black on top of head and sides of pronotum. Head: black from vertex onto rostrum; lateral ocelli large, median one very small, almost invisible; face and cheeks pale brown. Pronotum: dorsum pale brown, lateral lobes black in upper half, pale brown in lower half. Legs all pale. Abdomen pale brown.

SPECIMENS. *Holotype* M, HONOLULU. *Paratypes*: Col des Rousettes, 450 - 550 m, 4 ii 1963 (Gressitt) 1F, HONOLULU. Col d'Amieu, 650 m, 31 iii 1968 (Gressitt and Maa) 1F, PHILADELPHIA.

Archenopterus bouensis Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Mt. Koghi, forest on west slope of Mt. Bouo, 26 ii 1983 (Alexander, Cade & Otte). ANN ARBOR.

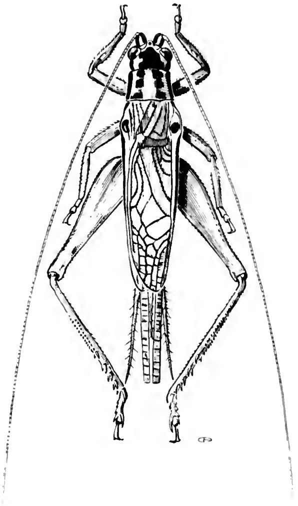


FIG. 39C. *Archenopterus maai* male.

RECOGNITION. Figs. 40F, 41D, 44B. Table 7. *Male*: Large for genus, very pale in color but with distinctive dark markings on pronotum and forewings. Head: dorusm reddish brown; scape yellow; face yellowish on frons, pearly white on clypeus and labrum; cheeks ivory. Pronotum: dorsum marked as in figure; lateral lobes ivory in lower quarter, dark brown in middle half, and yellow in upper quarter. Forewings: with huge forewing gland; color generally pale and translucent, but with dark brown veins; lateral field pale, dark brown around forewing gland. Hindwings extending approximately 1.5 pronotal lengths beyond forewings. Abdomen entirely pale. Legs all ivory colored.

SONG. Fig. 45.

HABITAT. Collected in forest undergrowth about 10 feet above the ground.

SPECIMENS. *Holotype* M, ANN ARBOR.

Archenopterus amoensis Otte, n. sp.

TYPE. *Holotype* M, New Caledonia, Amoa Valley, 7 ii 1963 (Krauss). HONOLULU.

RECOGNITION. Figs. 40D, 41E, 43B. Table 7. *Males*: Body pale, straw-colored. Head: dorsum reddish brown, with two pale stripes extending from rear margin of eyes to pronotum, also with a pale band running from inner margins of eye past lateral ocelli to level of median ocellus; face and cheeks pale. Pronotum: dorsum pale brown with ivory stripes along lateral margin; lateral lobes slightly darker than dorsum. Forewings: dorsum pale brown with large shallow forewing gland; lateral field pale brown, Sc with 6 branches. Hindwings extending 2 pronotal lengths beyond forewings. All legs uniformly pale brown. Hindfemora with black crescents of knee. Hind basitarsus with an extremely long inner apical spur, about as long as third tarsal segment.

Females: not known.

SPECIMENS. *Holotype* M, HONOLULU.

Archenopterus hemiphonus Otte, n. sp.

TYPE. *Holotype* M, New Caledonia, Col d'Amieu, 650 m, 21 iii 1968 (Gressitt). HONOLULU.

RECOGNITION. Figs. 41F, 44A. Table 7. *Males*: Body color gray-brown with yellow postocular stripe which continues on the pronotum and the forewings. Head: dorsum dark brown with a narrow yellow stripe from posterior inner margin of eye to pronotum and a yellow stripe running from the anterior inner margin of the eye through all three ocelli; face and cheeks pale, yellowish. Pronotum: dorsum dark brown, with yellow lateral bands; MAPs paler than surrounding areas; lateral lobes brown to dark brown. Forewings: gray with dark brown veins; with yellow stripe at lateral margins which is interrupted by the forewing gland and again at the midpoit of the forewing. Sc and R veins brown; M vein yellow before and after the forewing gland, then brown posterior of the point where it joins the R vein. Cu_1 brown to midpoint of wing, then yellow. Cu_2 not fully developed as a stridulum and with about 28 small teeth. Hindwings extend about two pronotal lengths beyond the forewings.

Females: not known.

SPECIMENS. *Holotype* M, HONOLULU.

APHONOIDES Chopard

Aphonoides Chopard 1940: 203. Type species: *Gryllus (Eneoptera) punctatus* Haan 1942: 232. Designated by Chopard 1968: 399.

This genus is known mainly from Australia and New Guinea. *Aphonoides ouveus* is thus far the only known member of the genus from this region of the Pacific. See Otte and Alexander (1983) for a discussion of this genus.

Aphonoides ouveus Otte, n. sp.

TYPE. *Holotype M*, Loyalty Islands, Ouvea, Fayaoue, 0 - 50 m, i 1969 (Krauss). HONOLULU.

RECOGNITION. Fig. 20C. *Males*: Body color pale straw-yellow. Head: Ocelli all large, nearly equal in size. Scape 2.0 times as wide as front of rostrum. Face and cheeks straw yellow. Pronotum, forewings, and legs straw yellow; dorsal field of forewings with 7 parallel veins besides Cu_1 vein. Hindwings extend 1.5 pronotal lengths beyond forewings. Foretibiae with 2 and midtibiae with 3 apical spurs; hind tibiae with 6 inner and 5 outer subapical spurs. Foretibiae with a large inner and no outer tympanal opening. Measurements of holotype and paratype (mm): BL, 12, 14; FL, 8.2, 9.0; FWL/PL, 6.0, - ; TL/FL, 0.92, -.

Females: Not known.

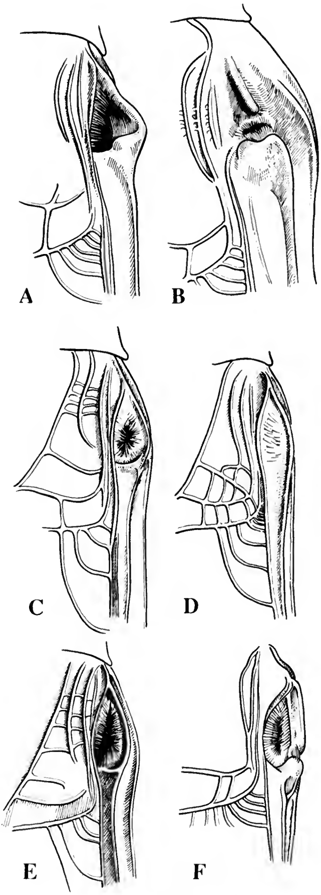


FIG. 40. A-F, *Archenopterus* male forewings showing forewing gland. A, *gressitti*. B, *hemipteroides*. C, *maai*. D, *amoensis*. E, *maai*. F, *bouensis*. G. *A. bouensis* holotype pronotum.

SPECIMENS. *Holotype* M, HONOLULU. *Paratype*: same locality but ii 1963 (Krauss) 1M, PHILADELPHIA.

CALSCIRTUS n. gen.

TYPE SPECIES: *Caledoscirtus amoa* Otte, n. sp.

RECOGNITION OF GENUS. Figs. 46-50. Table 8. Body slender, color pale brown to straw yellow. Rostrum very narrow. Fore- and midfemora very broad. Median ocellus tiny or obsolete. Head and pronotum covered with medium to dense pubescence. Pronotum appearing longer than wide, actually slightly wider than long; MAPs distinctly triangular; pronotal margins without very large bristles, but may have a dense growth of finer setae. Forewings extending beyond end of abdomen. Males with a stridulum and a well-developed mirror. Hindwings extending beyond forewings. Subgenital plate elongate but not coming to a narrow point as in *Adenopterus*. Tympanal openings on inner and outer faces, nearly equal in size. Foretibiae with 3 and midtibiae with 4 apical spurs. Hind tibiae with 5 inner and 5 outer subapical spurs and with 3 inner and 3 outer apical spurs. Spurs begin above middle of tibiae (they begin at or below this point in *Adenopterus* and *Archenopterus*.

Calscirtus amoa Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Amoa River, 3 km west of main road, near Poindimié, 3 iii 1983 (Alexander, Cade, and Otte). ANSP.

RECOGNITION. Figs. 47D, 48F, 49C, 50B. Table 8. Apical area of forewing shorter than mirror. Inner and outer subapical spurs on hind tibiae extending into apical half of tibia. Epiphallus deeply grooved at apex.

Males: Head: dorsum unpatterned, area between eyes and ocelli flat or slightly convex (not concave as in *timbiensis*; face and cheeks very pale. Pronotum: dorsum variegated pale brown and ivory; lateral lobes entirely pale. Abdomen: dorsum and venter pale brown; subgenital plate dark gray-brown, emarginate at distal end. Forewings: dorsal field lateral field. Hindwings extending one half PL beyond forewings. Legs: pale brown, Hindfemora with numerous pale brown oblique stripes; hind tibiae with 5 inner subapical spurs (*paniensis* with 3); hind basitarsus with 2 inner and 3 outer dorsal spines, two at apex. Cerci pale at base, dark brown through most of basal half, then pale.

BIOLOGY. Collected in a tree in a riverine forest.

SPECIMENS. *Holotype* M, PHILADELPHIA.

Calscirtus paniensis Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, Loc 27, ca. 17 km east of Oubatche, coastal forest, 6 iii 1983 (Alexander, Cade, and Otte). PHILADELPHIA.

RECOGNITION. Figs. 47F, 48C, 49A, 50A. Table 8. Epiphallus extremely wide; ectoparameres symmetrical.

Males: Head: dorsum slightly concave betwen eyes and lateral ocelli. Differing from other species mainly in size and by the male genitalia and in possessing only 3 inner subapical spurs. Subgenital plate dark brown. Hindwings extending about one pronotal length beyond forewings. Hind basitarsus with one inner and two outer dorsal spines.

BIOLOGY. Collected in low foliage of a 30 foot tree in a northeastern coastal forest. Other males were singing in higher trees.

SPECIMENS. *Holotype* M, PHILADELPHIA.

Calscirtus timbiensis Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, 2 km southeast of Timbia, Ngoue, 0 - 5 m, 20 ix 1979 (Gagné, Nishida, and Samuelson). HONOLULU.

RECOGNITION. Figs. 46, 47A, B, 48A, 49B, 50C, D. Table 8. Epiphallus very wide at base, then narrowing strongly at apex, with a small U-shaped apical notch; ectoparameres highly

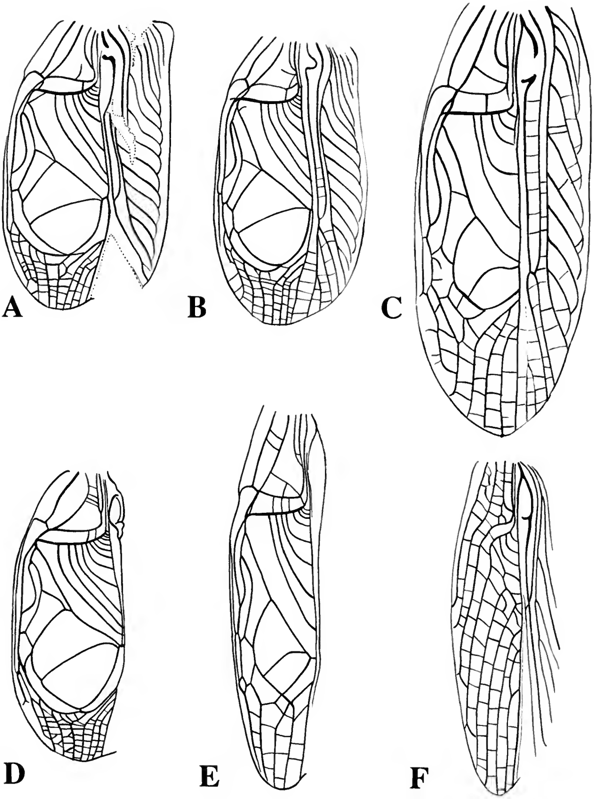


FIG. 41. *Archenopterus* male forewings. A, *hemipteroides*. B, *gressitti*. C, *maai*. D, *bouensis*. E, *amoensis*. F, *hemiphonus*.

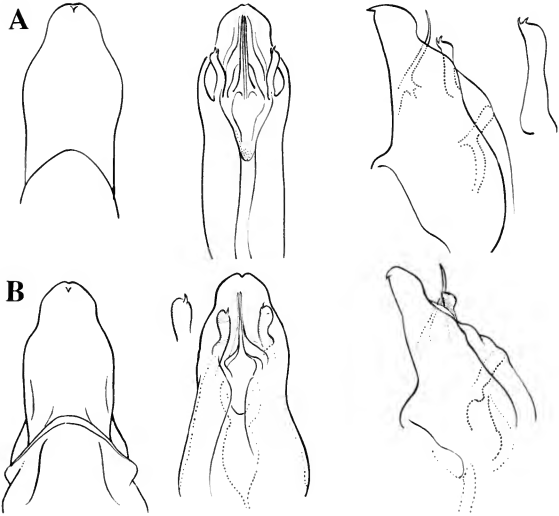


FIG. 42. *Archenopterus* male genitalia (holotypes). **A**, *gressitti*. **B**, *hemipteroides*.

Table 8. Comparison of Calscirtus species (see Methods for abbreviations).

	BL	FL	CL	FLW/PL	No. subapical spurs inner/outer
paniensis					
M	33	17	10.3	2.3	3/5
timbiensis					
M	24	13.3	10	4.4	5/5
M	23	12.6	10	4.7	5/5
koghi					
M	22	11.8	ca. 8.0	3.9	5/5

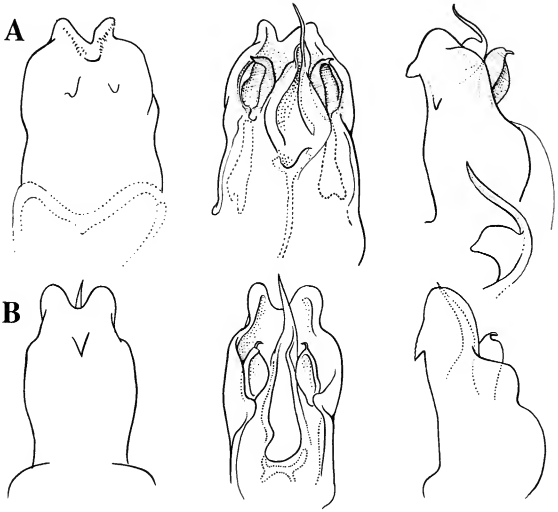


FIG. 43. *Archenopterus* male genitalia (holotypes). A, *maai*. B, *amoensis*.

asymmetrical with only right one developed into a spine.

Males: Head distinctly concave in region bounded by eyes and lateral ocelli. Hind tibiae with ca. 21 outer and 15 inner tibial spines. Hind basitarsus with 2 inner and 2 outer dorsal spines.

BIOLOGY. Collected in coastal forest.

SONG. Not known.

SPECIMENS. *Holotype* M, HONOLULU. *Paratypes*: La Foa, 3 ii 1945 (Milliron) 1M, HONOLULU. Mt Koghi, 420 m, 21 ix 1979 (Gagne, Nishida, and Samuelson) 1M, HONOLULU.

MATUANUS Gorochov

TYPE SPECIES: *Matuanus priapus* (Saussure)

RECOGNITION OF GENUS. Figs. 25E, 51-53. Table 8. Male genitalia symmetrical, epiphallus elongate, upturned at apex and coming to two small apical points; ectoparameres hinged at base, slender, and capable of moving ventrally or laterally with respect to epiphallus, terminating is a small hook; virga very stout. Forewings usually without a stridulum (if a stridulum is present the wing is otherwise simplified, showing loss of the mirror, harp and chords, e.g., *elegans*).

Body slender; male forewings without a mir-

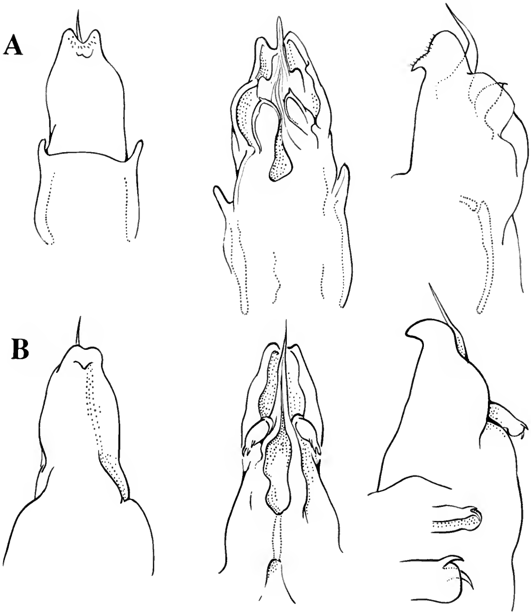


FIG. 44. *Archenopterus* male genitalia (holotypes). A, *hemiphonus*. B, *bouensis*.

ror; in one species (*elegans*) the male possesses a stridulum, in the other (*roussettes*) it does not. Rostrum relatively broad: 0.63 - 0.75 times width of antennal scape. Large tympanal openings on both inner and outer faces. Foretibiae with 3 and midtibiae with 4 apical spurs. Hind tibiae with 5 inner and 5 outer subapical spurs and 3 inner and 3 outer apical spurs. Subgenital plate tapering to a point, but not nearly as long as in *Adenopterus* or *Archenopterus*. TL/FL, 0.93 - 0.95; FW/FL, 0.26 - 0.28.

Matuanus priapus (Saussure)

Podoscirtus priapus Saussure 1877: 648. Types M and F, New Caledonia (Brunner de Wattenwyl, No. 5964). VIENNA. The types were not seen; the were requested but could not be located. The illustrations of *priapus* are from Gorochov (1986) and are presumed to be of this species.

Munda priapus, Chopard 1968: 411.

RECOGNITION. Fig. 52C.

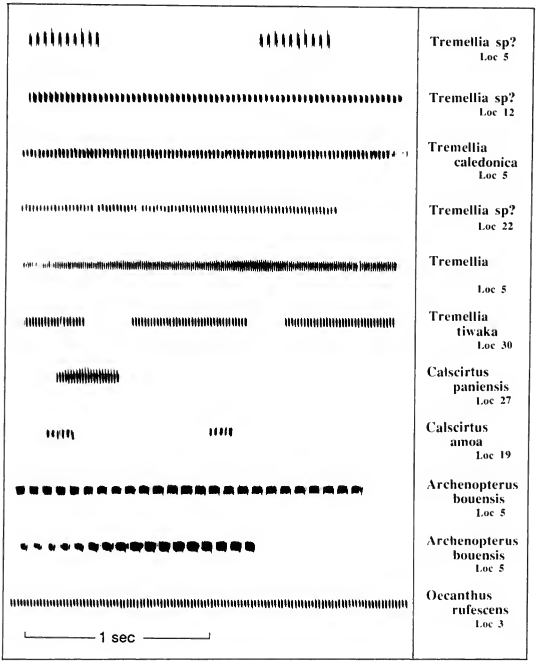


FIG. 45. Songs of *Tremellia, Calscirtus, Archenopterus* and *Oecanthus* species (Loc, locality).

Matuanus caledonicus (Saussure)

Aphonus caledonicus Saussure 1878: 658. *Holotype F*, New Caledonia (Brunner collection). VIENNA. *Aphonomorphus*, Kirby 1906: 105. *Aphonoides*, Chopard 1968: 401. Type examined. NEW COMBINATION.

RECOGNITION. Fig. 52B. Table 9. Virga of male genitalia extending beyond epiphallus, very wide and open at apex (most similar to *flavomaculatus* but apex of virga much wider and apex of ectoparameres more like a corkscrew).

Males: A dark reddish brown with pale line along the lateral margins of forewings. Head: dorsum rusty brown then black from midpoint of eyes to median ocellus; face reddish brown; cheeks rusty colored with a small yellow mark along lower-posterior margin of the eye; median ocellus very small. Forewings: dorsum with 9 or

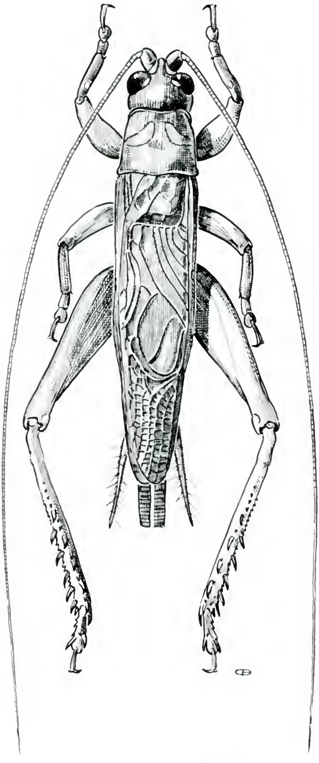


FIG. 46. *Calscirtus timbiensis* male.

10 parallel veins excluding Cu_1; veins dark brown, except pale brown to yellow along margins of dorsal field; lateral field blackish. Sc vein dark; R and M veins yellow throughout their length (R brown in *flavomaculatus*); Cu_1 vein brown in basal sixth, then yellow throughout remaining length; Cu_2 though about basal third. Hindwings extending about two pronotal lengths beyond forewings. All legs yellowish brown. Abdomen: subgenital plate tapering to a point, though not as long as in *Adenopterus.*

Females: very similar to males in color but larger.

SPECIMENS. *Holotype* M, VIENNA. *Paratypes*: Col des Roussettes, 450 - 550 m, 4 - 6 ii 1963 (Krauss) 1M, HONOLULU. Yiambi, NE, 0 - 50 m, 15 x 1967 (Sedlacek) 1F, HONOLULU. Valle de Thy, 250 - 500 m, 28 iii 1981 (Gressitt and McPherson) 1F, HONOLULU. Sarramea, 12 ii 1963 (Yoshimoto) 1M, HONOLULU. 25 km W of Canala, forest, 1 iii 1983 (Alexander, Cade, and Otte) 1F, PHILADELPHIA. Above Koné, road to Panaki, forest, 7 iii 1983 (Alexander, Cade & Otte #30) 1F, PHILADELPHIA. West of Ponerihouen, Mt Aopinie, 550 m, 30 vii 1971 (Gressitt) 1M, HONOLULU. Mokoue to Dothio, 150 - 500 m, 20 iii 1968 (Gressitt) 1F, HONOLULU. Hienghene, 0 - 100 m, i 1971 (Krauss) 1F, HONOLULU.

Matuanus elegans Otte, n. sp.

TYPE. *Holotype M*, New Caledonia, 25 km from Col de Roussettes, 6 ii 1963 (Krauss) PHILADELPHIA.

RECOGNITION. Figs. 25, 51, 52A. Table 9. Body patterned as figured. Virga long and tubular and with a tuft of hairs at the apex.

Males: Head: dorsum black posterior to median ocellus; face ivory colored, with a broad brown band descending to the clypeus. Pronotum: dorsum rusty colored; lateral lobes rusty colored in upper half, ivory in lower half. Forewings: with a stridulum but without a mirror; dorsal field with a row of ivory spots on black background along Cu_1 vein; spots located at junc-

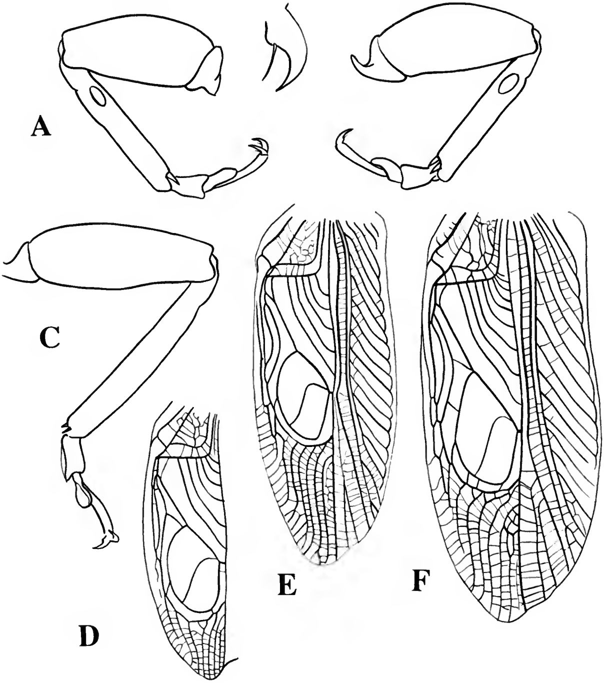


FIG. 47. *Calscirtus.* **A**, **B**, *timbiensis* foreleg (left, inner; right, outer). **C**, *timbiensis* midleg outer. **D**, *amoa.* **E**, *timbiensis.* **F**, *paniensis.*

tion of Cu_1 branches; also ivory along pronotal margin. Hindwings extending one half a pronotal length beyond forewings. Legs marked as in Fig. 51.

Females marked as in males. Occiput with 2 short pale longitudinal lines one either side of medial line. Posterior portion of pronotal disc becoming dark brown.

SPECIMENS. *Holotype* M, HONOLULU. *Paratypes*: Yahoue, 20 ii 1963 (Yoshimoto) 1M, HONOLULU; 60 - 100 m ii 1980 (Krauss) 1M, PHILADELPHIA. Col de Pitehikara, 300 - 450 m, 8 i 1969 (Krauss) 1M, HONOLULU. Mt. Panie, 8 ii 1963 (Krauss) 1M, HONOLULU. Pouebo, 26 i 1964

(Straatman) 1M, HONOLULU. Col d'Amieu, 650 m 31 iii 1968 (Gressitt and Maa) 1M, HONOLULU. Col de Rousettes, 450 - 550 m, 4 ii 1963 (Krauss) 1M, HONOLULU. Mt Koghi, 27 i 1963 (Yoshimoto) 1M, HONOLULU; ii 1962 (Krauss) 1M HONOLULU; i 1969 (Krauss) 1M, HONOLULU; 26 i 1963 (Yoshimoto and Krauss) 1M, PHILADELPHIA; ii 1973 (Krauss) 1F, PHILADELPHIA; 5 iii 1960 (Gressitt) 1F, HONOLULU; i 1969, 1F HONOLULU; 27 i 1963 (Yoshimoto) 1F HONOLULU; ii 1973 (Krauss) 1F, HONOLULU. Foret de Thi (or Thy), 100 - 200 m, 10 iii 1961 (Sedlacek) 1M PHILADELPHIA; 550 m, 6 iii 1960 (Gressitt) 1F HONOLULU; 100 - 300 m, 25 iii 1961 (Sedlacek) 1F, HONOLULU. Poindimie, 11 ii 1963 (Krauss) 1M HONOLULU. Col d'Amieu, 750 m, 3 iii 1960 (Gressitt) 1F, HONOLULU. 25 km from Col de Rousettes, 6 ii 1963 (Krauss) 1F, HONOLULU. Col de Pirogue, 14 ii 1963 (Krauss) 1F, HONOLULU. Col de Rousettes, 4 ii 1963 (Krauss) 1F, HONOLULU. La Foa-Canala saddle, 480 - 500 m, 30 i 1963 (Yoshimoto) 1F, HONOLULU. Koné,

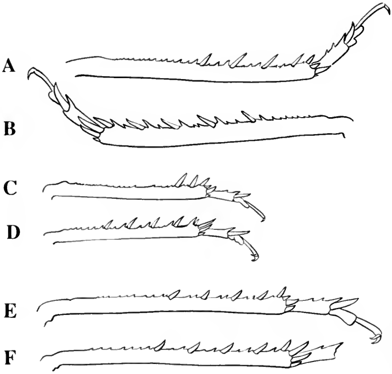


FIG. 48. *Calscirtus* hind tibiae. **A**, *timbiensis* outer; **B**, inner. **C**, *paniensis* outer; **D**, inner. **E**, *amoa* outer; **F**, inner.

Table 9. Comparison of Matuanus species. V, number of parallel veins on dorsum of forewings (not including Cu1). See Methods for abbreviations.

	BL	FL	CL	FWL/PL	OL/FL	V
caledonicus						
5M	14-18	11-12	8-9	5.7-6.4	-	8-10
6F	18-21	12-14	11.5-13.5	6.3-6.7	0.89-0.97	9
flavomaculatus						
HM	14	9.4	7	5.9	-	8
PM Plum	14.5	10.2	8	6.3	-	8
PM Plum	13	8.2	-	6	-	9
PF Paita	17	-	12	6.6	-	10
PF I. Pines	17.3	12.1	12	6	0.93	9
PF Koghi	18	11.7	11.1	7.3	0.98	8
PF Yahoue	17	13	12	6.4	0.96	9
PF Mt Mou	17	11.5	-	5.9	1.07	8
neoplumas						
HM	14	-	-	5.9	-	9
rufidulus						
HF	11.7	-	5	0.79	-	
elegans						
5M	18-21	13-14	11-12	5.8-6.4	-	10-14
5F	23-27	15-17	12-16	6.2-6.3	0.76- 0.87	

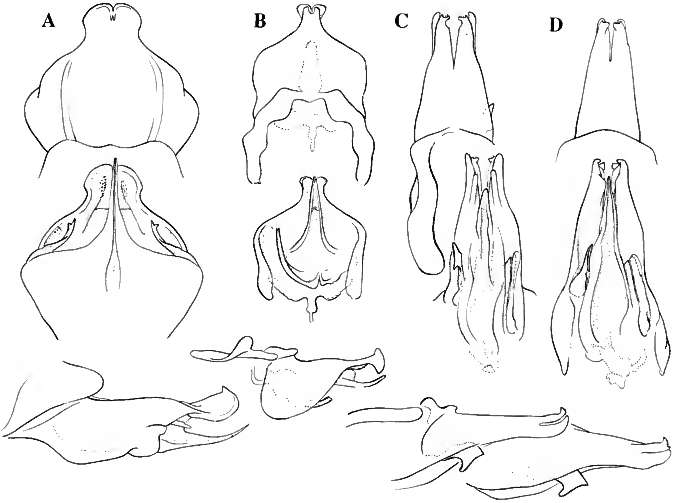


FIG. 49. *Calscirtus* male genitalia (holotypes). **A**, *paniensis*. **B**, *timbiensis*. **C**, *amoa*.

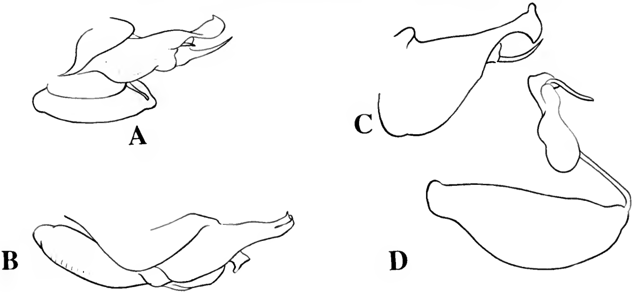


FIG. 50. *Calscirtus*. **A**, *paniensis* male genitalia showing position of spermatophore. **B**, *amoa* genitalia showing position of spermatophore. **C**, **D**, *timbiensis* showing angle of spermatophore before it is removed.

mountain forest, road to Panaki, 7 iii 1983 (Alexander, Cade and Otte) 1F, PHILADELPHIA.

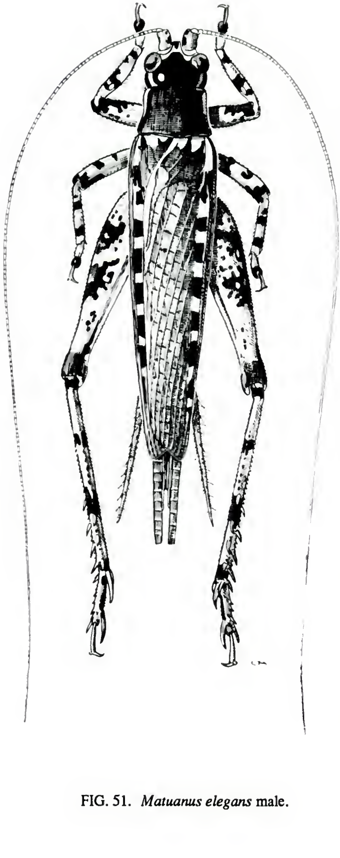


FIG. 51. *Matuanus elegans* male.

Matuanus rufidulus (Saussure)

Podoscirtus rufidulus Saussure 1878: 648. *Holotype F*, La Nouvelle-Calédonie (Collect. de M.Brunner de Wattenwyl). VIENNA. *Podoscirtus*, Kirby 1906: 104. *Munda*, Chopard 1968: 411. Type examined. NEW COMBINATION.

NOTES ON HOLOTYPE. Table 9. Body color pale orange brown; pronotum reddish. Head: dorsum orange brown with slightly darker areas between eyes and on rostrum; face orange-brown, with dark markings at upper end of frons; cheeks with a dark area near lower margin. Pronotum: dorsum reddish; lateral lobes orange-brown. Forewings uniform in color, with 10 parallel veins. Hindwings extending about one pronotal length beyond forewings. Foretibiae with large inner and outer tympana. Foretibiae with 3 and midtibiae with 3 apical spurs. Legs uniform pale orange-brown. Hind tibiae with 5 inner and 5 outer subapical spurs. Crescents of hind knees black.

Matuanus flavomaculatus Gorochov

Matuanus flavomaculatus Gorochov 1986: 705. *Holotype F*, New Caledonia, Mt. Koghi. LENINGRAD.

RECOGNITION. Fig. 52. Table 9. Virga of male genitalia extending to end of epiphallus, but narrow and pointed at apex; (apex of virga narrow and apex of ectoparameres more like a small beak).

Males: Similar to *caledonicus*. Body color dark reddish brown, legs paler. Dorsal field of forewings yellow at base and along margins. Head: dorsum reddish brown, black between vertex and median ocellus; with narrow yellow stripe running from posterior of eyes to pronotum; face reddish brown, with two yellow markings between lower margins of antennal

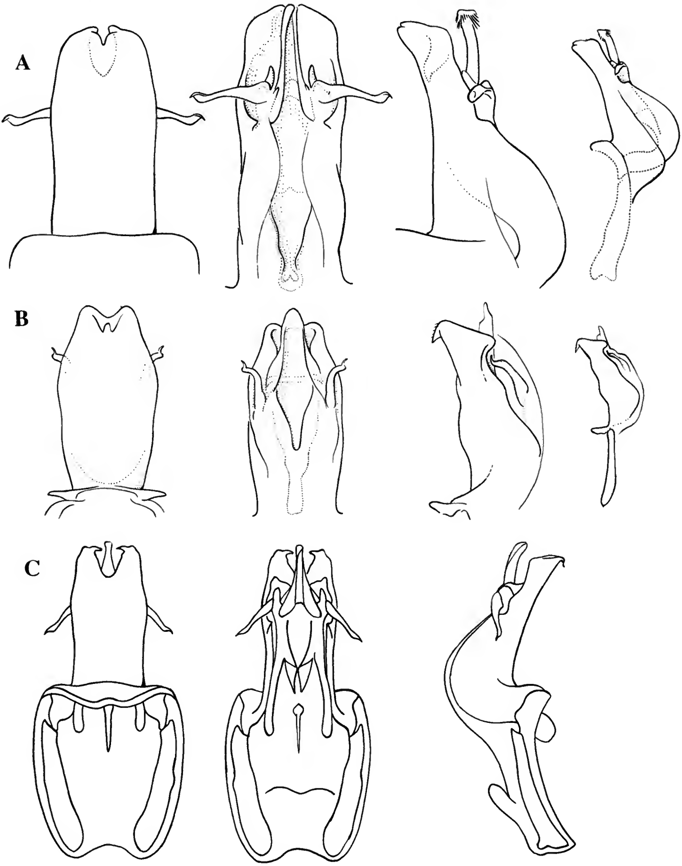


FIG. 52. *Matuanus* male genitalia (holotypes). A, *elegans*. B, *caledonicus*. C, *priapus*.

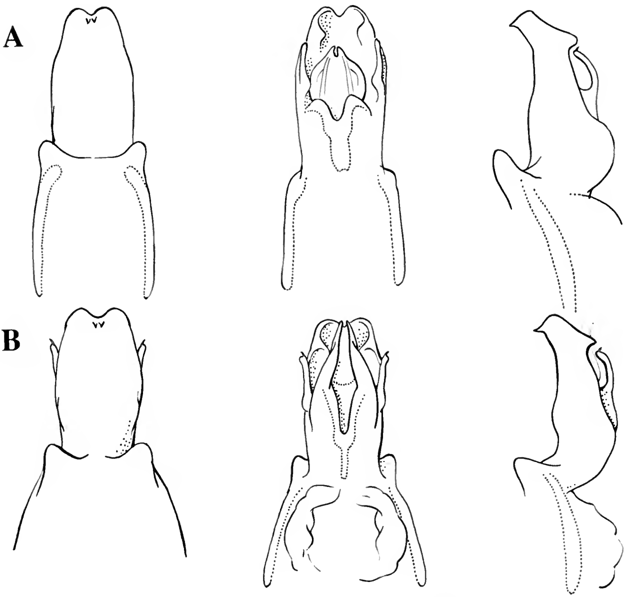


FIG. 53. *Matuanus* male genitalia (holotypes). A, *neoplumus*, B, *flavomaculatus*.

sockets and with a yellow marking along lower posterior margin of the eyes. Pronotum: unicolorous dark reddish brown. Forewings: dorsum dark brown, each forewing with a large yelllow marking at base (includes bases of Cu_2, 1A, 2A, and 3A veins), and with a yellow streak along the lateral margins. Sc vein brown, Sc branches also brown at base then becoming yellow ventrally in some specimens; R vein brown, M vein and area between R and M yellow; Cu_1 vein brown in basal sixth, then yellow. Legs all orange-brown. Hindfemora orange-brown, darker on knees. Foretibiae with 3 and middle tibiae with 4 apical spurs; hind tibiae with 5 inner and 5 outer subapical spurs.

Females: very similar to males, but larger.

SPECIMENS. *Holotype* M, LENINGRAD. New Caledonia, St. Louis Valley, 17 iii 1945 (H. E. Milliron) 1M, HONOLULU. Between Plum and Yati, 25 iii 1968 (Gressitt) 1M, PHILADELPHIA. 6 km north of Paita, 25 i 1963 (Yoshimoto) 1F, HONOLULU. Isle of Pines, iii 1959 (Krauss) 1F, HONOLULU. Mt Koghi, 500 m, 27 x 1967 (Sedlacek) 1F, HONOLULU. Yahoue, 60 - 100 m, ii 1969 (Krauss) 1F, HONOLULU. Mt Mou, 11 ii 1962 (Krauss) 1F, HONOLULU. Mt. Koghi, Foret de

Thi, 530 m, 8 iii 1961 (Sedlacek) 1F, HONOLULU. La Coulee, 23 i 1963 (Krauss) 1F, HONOLULU. St. Louis, viii, 1M, HONOLULU. 10 km NW Plum, 24 iii 1968 (Gressitt and Maa) 1M, HONOLULU.

Matuanus neoplumus Otte, n. sp.

TYPE. *Holotype M*, Yahoue, 22 i 1963 (Yoshimoto). HONOLULU.

RECOGNITION. Fig. 52. Table 9. Very similar to *caledonicus* but virga short and wide, not extending beyond the ectoparamers.

Males: Body color dark reddish brown, with yellow lateral stripes. Head: occiput reddish brown, black from vertex to median ocellus; with a narrow yellow stripe behind each eye; median ocellus about one third the size of the lateral ocellus; face reddish brown; cheeks with a small yellow spot at lower posterior margin of eyes. Pronotum uniform reddish brown. Forewings: dorsum gray brown with darker veins; anterior end with large yellow patch at bases of Cu_2, 1A, 2A, and 3A. Sc and R veins brown, M vein bright yellow in basal third, then less bright over remaining length. Cu_1 vein brown in basal quarter then yellow through remainder. Fore- and midlegs orange-brown. Hindlegs lost. Hindwings extending two pronotal lengths beyond the forewings.

Females: not known.

SPECIMENS. *Holotype* M, HONOLULU.

LITERATURE CITED

BALLANCE, P. F. (ed.). 1980. Plate tectonics and biogeography in the southwest Pacific: the last 100 million years. Paleogeography, Paleoclimatology and Paleoecology 31(2-4): 101-372.

CHOPARD, L. 1915. Gryllidae de la Nouvelle-Calédonie et des Iles Loyalty. F. Sarasin & J. Roux (ed) Nova Caledonia, Zoologie Vol. II, No. 8. C. W. Kreidels Verlag, Wiesbaden.

CHOPARD, L. 1967. Orthopterorum Catalogus. Pars 10. W. Junk, Gravenhage

CHOPARD, L. 1968. Orthopterorum Catalogus. Pars 12. W. Junk, Gravenhage

CHOPARD, L. 1970. Ergebnisse der Österreichischen Neukaledonien-Expedition 1965. Neue und wenig bekannte Orthopteren aus Neukaledonien. II. Gryllodea. Ann. Naturhistor. Mus. Wien 74: 285-288.

GOROCHOV, A. V. 1986. New and little known crickets (Orthoptera, Gryllidae) from Australia and Oceania. Revue d'Entomologie de l'URSS 65 (4): 692-708.

GRESSITT, J. L. 1961. Problems in the zoogeography of Pacific and Antarctic insects. Pacific insects Monograph 2: 1-127.

HOLLOWAY, J. D. 1979. *A survey of the Lepidoptera, Biogeography and Ecology of New Caledonia.* Dr. W. Junk, The Hague.

KROENKE, L. W. 1984. Cenozoic tectonic development of the Southwest Pacific. U.N. ESCAP, CCOP/SOPAC Techical Bulletin 6: 1-123.

COLEMAN, P. J. 1980. Plate tectonics background to biogeographic development in the Southwest Pacific of the last 100 million years. Paleogeography, Paleoclimatology and Paleoecology 31(2-4): 105-122.

OTTE, D. AND R. D. ALEXANDER. 1983. *The Australian Crickets*. Academy of Natural Sciences Monograph 22: 1-477.

OTTE, D. AND D. C. RENTZ. 1985. The crickets of Lord Howe and Norfolk Islands (Orthoptera, Gryllidae). Proceedings of the Academy of Natural Sciences of Philadelphia 137(2): 79-101.

SAUSSURE, H. DE. 1878. Mélanges orthoptérologiques, 6e fasc., Mém. Soc. Genève, XXV: 369-696.

THORNTON, I. W. B. 1980. Plate tectonics and the distribution of the insect family Philotarsidae (Order Psocoptera) in the Southwest Pacific. Paleogeography, Paleoclimatology and Paleoecology 31(2-4): 251-266.

Proceedings of The Academy of Natural Sciences of Philadelphia 139: 459-463, 1987

Gymnothorax baccaladoi, a new Moray from the Canary Islands (Pisces: Muraenidae)

EUGENIA B. BÖHLKE
Department of Ichthyology
Academy of Natural Sciences of Philadelphia
19th and The Parkway, Philadelphia, PA 19103

ALBERTO BRITO
Departamento de Biologia Animal (Ciencias Marinas)
Facultad de Biologia, Universidad de La Laguna,
Tenerife, Canary Islands

ABSTRACT.— A new moray from the Canary Islands,with mottled brown coloration, the posterior jaw pores set in white spots, and serrate teeth, is described and illustrated. It is tentatively assigned to the genus *Gymnothorax*, sensu lato. It differs from most morays in possessing only one branchial pore, and differs from other Atlantic species of *Gymnothorax* in its biserial maxillary and vomerine dentition [Atlantic, Canary Islands, *Gymnothorax bacalladoi*, moray, Muraenidae, new species]

Atlantic species of the eel family Muraenidae have been the subject of extensive studies by the senior author and others during the past decade (Böhlke, McCosker, and Böhlke in press). As these studies were nearing completion in March, 1986, a small, dark moray with serrate teeth, collected in the Canary Islands, was sent by the junior author for identification. His suspicion that it might be a new species was confirmed, and two additional specimens were subsequently obtained. In external appearance, it closely resembles other species of *Gymnothorax*; however, it differs from other Atlantic species in its unique dentition: biserial maxillary teeth, the rows short, outer teeth triangular and serrate, inner teeth long, slender and smooth-edged; and two rows of short, almost molariform, vomerine teeth. In addition, it differs from other morays (with the exception of the monotypic genus *Monopenchelys*) in having only one lateral line pore in the branchial region.

Measurements are straight line, made with a ruler or with dial calipers. Head length is measured from the snout tip to the posterodorsal margin of the gill opening. Body depth does not include the median fins. Vertebral counts (which include the hypural) were obtained from radiographs, methods and terminology following that of Böhlke (1982). The type specimens are deposited at the Academy of Natural Sciences of Philadelphia (ANSP), the California Academy of Sciences, San Francisco (CAS), and the Museo de Ciencias Naturales de Santa Cruz de Tenerife, Canary Islands (TFMC).

Gymnothorax bacalladoi n. sp.
Figs. 1-3, Table 1

DIAGNOSIS. A moderately elongate moray of the genus *Gymnothorax*, with: mottled brown coloration, posterior jaw pores in white spots; dorsal-fin origin before gill openings; four infraorbital pores, one branchial pore; outer teeth serrate, maxillary teeth in two short rows, and vomerine teeth biserial; and mean vertebral formula (MVF) 5-55-130.

COUNTS AND MEASUREMENTS (IN MM) OF THE HOLOTYPE. Total vertebrae 130; predorsal verte-

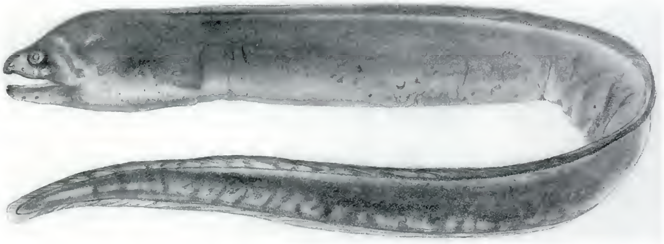


Fig. 1. *Gymnothorax bacalladoi*: ANSP 159041, paratype, 347 mm TL.

brae 5; preanal vertebrae 54. Head pores: supraorbital 1 (ethmoid) + 2; infraorbital 4; mandibular 6; branchial 1.

Total length 260; predorsal length 18.9; preanal length 125; head length 29.5; body depth at gill opening 14.5; body depth at anus 10.3; body width at gill opening 9.1; body width at anus 8.5; snout 4.65; upper jaw 10.9; lower jaw 10.9; eye diameter 2.7; interorbital width 3.0.

DESCRIPTION. See Table 1 for ranges of counts and proportions of the holotype and two paratypes.

Body elongate, laterally compressed, with tapering tail. Dorsal-fin origin on head, about midway between rictus and gill opening; anal fin beginning just behind anus, which is at or slightly before midbody. Head elevated and muscular; snout and jaws short, upper and lower jaws about equal. Eye moderate, above midjaw. Anterior nostril in narrow tube, directed anterolaterally; posterior nostril a raised rimmed pore above anterior half of eye.

Head pores developed, with irregular or elliptical rims (Fig. 2). Ethmoid pore on under side of snout; two supraorbital pores on dorsal surface of snout, the first above anterior nostril, the second between anterior pore and posterior nostril, closer to anterior pore. Four infraorbital pores; the first below and behind anterior nostril, the second midway between anterior pore and anterior margin of eye, the third below mideye, the fourth below posterior margin of eye. Six mandibular pores along lower jaw between jaw tip and rictus, the first at tip of jaw and elevated. The single branchial pore before and slightly above level of gill opening, below dorsal-fin origin; one specimen (ANSP 159041) with two pores on right side only (the usual condition in species of *Gymnothorax*). Gill opening a small oval opening, longest laterally, situated slightly below midside.

Teeth strong, the outer teeth serrate. On upper jaw, an anterior median tooth followed on each side by five outer intermaxillary teeth, increasingly larger posteriorly; these teeth stout, triangular, and canted back, the posterior margin strongly serrated and with basal knob. Maxillary teeth in two short rows; outer row of 14-27 close-set, triangular, serrate teeth of uniform size; inner row of 14-18 well-spaced, long, narrow, smooth teeth. On midline of upper jaw, one or two long, slender smooth fangs anteriorly, these teeth the longest in the mouth; on vomerine shaft, 9-15 low, conical, unequal teeth in two rows (sometimes staggered at the ends), reaching to or just beyond posterior end of maxillary tooth rows.

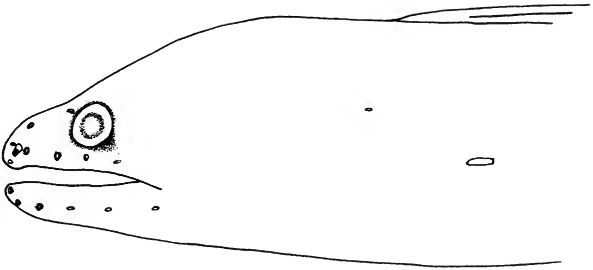


Fig. 2. *Gymnothorax bacalladoi*: ANSP 159041, paratype, 347 mm TL; head, showing nostrils and placement of head pores.

Dentary teeth uniserial; 10-16 strong, triangular teeth, largest anteriorly; teeth serrate, the serrations stronger on posterior margin, posterior basal knob present on anterior teeth.

COLOR. Body and fins brown, with pale and dark mottled areas; margins of fins dark, blackish posteriorly. Head brown; conspicuous dark ring around margin of eye; dark pigmentation on anterior nostril, at mouth angle, around gill opening and anus, and around anterior head pores (supraorbital pores, first two infraorbital and first three mandibular pores); inside of mouth pigmented. Posterior jaw pores (third and fourth infraorbital pores, last two mandibular pores) in conspicuous white spots. The holotype, the smallest specimen, has a prominent pale nuchal band on the dorsal surface of the head just behind the rictus, and dark longitudinal folds alternating with pale blotches in the branchial area.

SIZE. The largest of the three specimens is 347 mm TL. None, however, has mature gonads, and the species probably grows to a larger size.

DISTRIBUTION. The three known specimens are all from the Canary Islands. The holotype was captured in a bow net on the rocky bottom at 604 m; the paratypes were captured by hook at night at 17-20 m, also over rocky bottom. The locality of the holotype suggests that *Gymnothorax bacalladoi* may inhabit deep waters; if so, additional specimens might be collected by trap and longlines.

REMARKS. The most distinguishing feature of *Gymnothorax bacalladoi* is the single branchial pore; most muraenids possess two pores in the branchial region (although the genus *Monopenchelys* is distinguished by having only one such pore), and almost all species placed in *Gymnothorax* possess two branchial pores (*G. afer* differs from other Atlantic species in having 3 or 4 branchial pores).

The new species is tentatively placed in the genus *Gymnothorax*, based on its general appearance and because it possesses characteristics defining the genus: dorsal-fin origin on head midway between gill opening and rictus, anterior nostril tubular, posterior nostril nontubular, four infraorbital pores, and teeth strong, pointed, some caniniform. We define the genus in its broadest sense, and, in the Atlantic, include species previously placed in the genera *Gymnothorax*, *Lycodontis*, *Muraena* (*miliaris* only), *Neomuraena* and *Priodonophis*. *Gymnothorax bacalladoi* differs considerably from other Atlantic and Mediterranean species, and may be

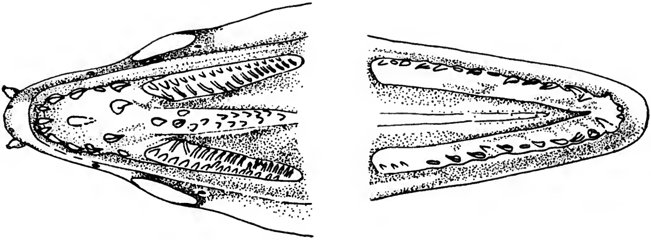


Fig. 3. *Gymnothorax bacalladoi*: ANSP 159041, paratype, 347 mm TL; dentition.

subgenerically, if not generically, distinct. However, generic limits and relationships cannot be established until a worldwide study of *Gymnothorax*, sensu lato (including Indo-Pacific species placed in related genera) is undertaken.

The general appearance and body shape of *Gymnothorax bacalladoi* is typical of other *Gymnothorax* with serrate teeth. In addition to the branchial pore condition, it differs from described species in coloration and dentition. The color combination of a dark body with both dark and pale mottlings and the posterior jaw pores in white spots differs from all other species of *Gymnothorax*. The dentition, in particular the very short maxilla and biserial maxillary dentition, differs from that of all species found in the Atlantic; it is most similar to that of the eastern Pacific *G. panamensis*, but *panamensis* has the dorsal-fin origin well behind the gill openings (above vertebrae 8-12), while *G. bacalladoi* has the "typical" *Gymnothorax* position above vertebrae 5-6. The short maxilla is similar to that found in some IndoPacific species previously placed in the genera *Siderea* and *Rabula* (excluding the species *Rabula acuta*), but they do not possess serrate teeth.

ETYMOLOGY. Named in honor of Dr. J. J. Bacallado for his notable contribution to the study of the marine fauna of the Canary Islands. A noun in the genitive case.

STUDY MATERIAL. *Holotype*. TFMC (ZM-2) (260 mm TL, immature); Canary Islands, Tenerife Island, Barranco Hondo, captured with the crustaceans *Plesionika edwardsi* (Brandt), *Paromola cuvieri* (Risso), and *Cancer bellianus* Johnson, by means of a bow net placed on rocky bottom at 604 m; G. Dionis; 10 Mar 1981.

Paratypes. ANSP 159041 (1, 347) and CAS 60405 (1, 287); Canary Islands, Tenerife Island, Puerto de Santa Cruz, captured with hook in the night over rocky bottom, depth 17-20 m; F. de Armas; Jan 1987.

ACKNOWLEDGEMENTS

Illustrations were prepared by Mary H. Fuges. Studies by the senior author have been partially supported by National Science Foundation Grant BSR 83-00279. We wish to thank Gustavo Dionis and Fernando de Armas (TFMC) for making the specimens available to the authors; John E. McCosker (CAS) for providing information on comparable Indo-Pacific species, and McCosker, David G. Smith (Harvard University), and William F. SmithVaniz (ANSP) for critical reading of the manuscript.

LITERATURE CITED

BÖHLKE, E. B. 1982. Vertebral formulae for type specimens of eels (Pisces: Anguilliformes). Proceedings of the Academy of Natural Sciences of Philadelphia, 134: 31-49.

BÖHLKE, E. B., J. E. McCOSKER, AND J. E. BÖHLKE. In press. Family Muraenidae. *In* Fishes of the western North Atlantic. Memoir Sears Foundation for Marine Research, No. 1, (9).

Table 1. Counts and proportions (in thousandths of TL or HL) of the holotype and two paratypes of *Gymnothorax bacalladoi* new species.

	Range	Mean
Total length (mm)	260-347	298.0
Predorsal vertebrae	5-6	5.3
Preanal vertebrae	54-56	55.0
Total vertebrae	130-131	130.3
Proportion of TL		
Head	112-122	116.0
Predorsal	72.6-101	86.2
Preanal	481-502	493.0
Tail	498-519	507.0
Depth at gill openings	55.8-71.1	63.0
Depth at anus	39.6-44.7	42.7
Width at gill openings	35.0-37.6	36.1
Width at anus	29.7-33.8	32.1
Proportion of HL		
Snout	149-173	160.0
Upper jaw	358-369	363.0
Eye	91.5-99.5	96.7
Interorbit	102-130	118.0

Proceedings of The Academy of Natural Sciences of Philadelphia 139: 465-526, 1987

The Succineid Snail Fauna of Chittenango Falls, New York: Taxonomic Status with Comparisons to Other Relevant Taxa

K. ELAINE HOAGLAND AND GEORGE M. DAVIS
The Academy of Natural Sciences, 19th and the Parkway, Philadelphia PA 19103

ABSTRACT.— In order to determine the relationships between *Succinea ovalis* Say, *S. ovalis chittenangoensis* Pilsbry of Chittenango Falls, New York, and specimens of uncertain affinity from Minnesota, electrophoretic studies of allozymes were conducted. *Oxyloma retusa* Lea and *O. decampi gouldi* Pilsbry of Chittenango Falls were included in the analysis for comparison. Via electrophoresis and shell morphometrics, we found yet another taxon at Chittenango Falls, *Succinea* sp., with shell shape similar to *Succinea putris* (Linnaeus) of Europe. Subsequent collection yielded two unknown species discovered by noting differences in mortality rate in the laboratory, considerable anatomical differences, and later, electrophoretic data. Anatomical studies were done on the above *Succinea*, including *S. putris* of Holland, and a population of *Succinea* from Philadelphia that also has a shell shape similar to *S. putris*. Because we could not find living topotypical *S. ovalis* from Philadelphia, we dissected topotypical material collected in 1923 to confirm the anatomy of *S. ovalis*. *Succinea chittenangoensis* is indistinguishable electrophoretically from *S. ovalis*, but has anatomical and shell–morphological differences worthy of species status. The Minnesota specimens belong to two closely-related taxa, probably subspecies, that in turn are specifically distinct from but in the same species group as *S. ovalis* and *S. chittenangoensis*. These taxa are relegated to the genus *Novisuccinea* Pilsbry. The two *Oxyloma* taxa group as a genus distinct from *Succinea*, as expected. Based on electrophoresis, the *Succinea* spp. of Chittenango Falls and Philadelphia are members of Succinea s.s., more closely related to *Oxyloma* than to *Novisuccinea*. Within *Succinea* s.s., one population from New York was referrable to *S. pennsylvanica* Pilsbry; the other, along with the population from Philadelphia, grouped with the *S. putris* species complex. We conclude that *N. chittenangoensis* is a valid species and a member of the *N. ovalis* species complex along with the species from Minnesota. *S. putris* in Europe is probably a species complex, i.e. a superspecies, with some members found in North America. [allozymes, anatomy, endangered species, introduced species, Minnesota, New York, Pennsylvania, Succineidae, *Succinea ovalis chittenangoensis*, *Succinea putris*, systematics]

ACKNOWLEDGMENTS

This research was supported by the New York State Department of Environmental Conservation, Endangered Species Unit, contract C000635 to the Academy of Natural Sciences and contract S001279 to Lehigh University. Specimens, reports and notes, and field assistance were provided by P. Riexinger and A. Breisch of that department. E. Thomée provided knowledge of habitats and allowed us to study her shell material and slides. Technical assistance involving the molecular genetics was given by C. Hesterman and A. Zacco; M. Ziegenfuss and M. McKey assisted with photography. G. Davis prepared the drawings, which were rendered by N. Karnow. Dr. E. Gittenberger arranged for us to receive specimens from the Rijksmuseum van Natuurlijke Historie, Leiden. Specimens were also received from Leslie Hubricht; all specimens associated with the project have been curated into the collections of The Academy of Natural Sciences. We are indebted to Dr. Ken Emberton for a critial review of the manuscript. This is a contribution from the molecular genetics laboratory of the Department of Malacology, The Academy of Natural Sciences of Philadelphia.

Henry Pilsbry collected succineid snails from Chittenango Falls, Madison County, N.Y., in August of 1905. From this material he described *Succinea ovalis chittenangoensis*, a new subspecies (Pilsbry 1908). He also identified *Succinea ovalis* Say s. s. from Chittenango Falls and *Oxyloma retusa* Lea from the town of Cazenovia in Madison County. The major distinctions between *S. ovalis* and its subspecies as defined by Pilsbry were the smaller size, shorter spire, and fewer number of whorls of *S. ovalis* (Pilsbry 1948).

Since Pilsbry's description, Hubricht (1972) and Grimm (1981) among others have considered *Succinea chittenangoensis* to be a distinct species. Solem (1976), on the other hand, called *S. chittenangoensis* a "marked genetic mutation of *S. ovalis*," based on his studies of anatomy of the reproductive system and radula.

The species status and population genetic structure of *Succinea o. chittenangoensis* is important because the taxon has been found only in the immediate vicinity of Chittenango Falls, in Chittenango Falls State Park, an area subject to physical destruction of the habitat by human trampling. The waters of Chittenango Creek and its falls are also subject to pollution, primarily from sewage. The New York State Department of Environmental Conservation has treated *S. chittenangoensis* as an endangered species and has prepared a recovery plan for it (Riexinger et al. 1983). Aloi and Ringler (1982) and Aloi (1986) have conducted population studies.

The purpose of the research described here was to determine if *Succinea o. chittenangoensis* is a valid species and if it is endemic to Chittenango Falls. First, the genetic relationships between *Succinea ovalis* and *S. o. chittenangoensis* of the Chittenango Falls area were analyzed. If *S. ovalis* and *S. o. chittenangoensis* could be found sympatrically and were fixed for alternate alleles at one or more loci, the distinct species status of *S. o. chittenangoensis* would be supported. When more taxa of uncertain affinity were discovered in Chittenango Falls, the study was expanded to include them and their possible European relative, *S. putris*. Specimens with shells similar to *S. o. chittenangoensis* from other localities were sought and analyzed electrophoretically, including two shell types from Minnesota. When questions remained that could not be solved using electrophoretic data, anatomical studies were done on all the *Succinea* sensu lato to provide additional necessary taxonomic information.

The genetic distances between the taxa are calculated and compared with the genetic distance between *Succinea ovalis* and two *Oxyloma* spp. from Chittenango Falls. On the basis of allozymes, anatomy, and shell characters, conclusions on the systematic status and endangered-species status of the New York and Minnesota taxa are drawn. The data support the allocation of the nine taxa studied to three genera: *Oxyloma*, *Novisuccinea*, and *Succinea*. *Succinea ovalis* and *S. o. chittenangoensis* are relegated to *Novisuccinea.*

LOCALITIES

Snails of the family Succineidae were collected July 27-29, 1983, by P. Riexinger at four localities:

1. Chittenango Falls, Town of Fenner, Madison County, New York, 75°50' 30" W, 42°58' 45" N. Specimens were taken from vegetation covering talus lying on the ledge located mid-level on the falls. Vegetation included *Nasturtium officinale*, *Myosotis scorpioides*, *Rhus radicans*, and several mosses. Specimens were also collected at the lower face of the falls on rock, talus, and vegetation including mosses, liverworts, *Angelica atropurpurea*, *Eupatorium purpurem*, and *Symplocarpus foetidus*. Specimens from the two sites were pooled.

2. A spring located 25 m north of the base of Chittenango Falls yielded specimens of Succineidae on *Nasturtium officinale* and *Myosotis scorpioides*.

3. East side of Route 13, 6.4 km north of Chittenango Falls, 3.1 km south of the intersection of Routes 5 and 13 in the Village of Chittenango, Town of Fenner, Madison County, New York, 75° 51' 35" W, 43° 1' 45" N. Specimens were found 160 m east of Chittenango Creek in

Table 1. Specimens from Chittenango Falls and environs. Sample size for electrophoresis and ANSP catalog number (in parentheses)

	Population			
Species	Falls	Watercress	Fenner	Sullivan
Succinea				
cf. *pennsylvanica* [a] (1985)	-	15(A11609A)	-	-
sp. B [b] (1983)	11(358242)	-	-	-
sp. B [b] (1985)	12(A11609B)	16(358244)	-	-
Novisuccinea				
chittenangoensis [c]	23(358243; A11609C)	1	-	-
ovalis [d]	-	-		15(358245)-Electr. A11609D-Anat.
Oxyloma				
retusa	1(358241)	-	16(358247)	79(358246)
decampi gouldi	16(358240)	-	-	-

[a] tall-spired; flat-sided whorls, shallow suture, small; golden color spire (coded H_1).
[b] tall-spired; flat-sided whorls, shallow suture, large; grey spire (coded H_2).
[c] tall-spired; round-shouldered whorls, deep suture.
[d] short-spired.

the flood plain of the creek downstream of the falls. The area contained a dense *Typha angustifolia* marsh of 2 ha over saturated soil, interspersed with narrow, shallow rivulets.

4. North of Routes 5 and 13, immediately east of the Village of Chittenango, 0.8 km east of the intersection of Routes 5 and 13 in the Village, 10.3 km north of Chittenango Falls, Town of Sullivan, Madison County, New York, 75° 51' 15" W, 43° 3' 20" N. The collection site is 1.1 km east of Chittenango Creek downstream of the falls. The habitat was a dense *Typha latifolia* - *Typha angustifolia* marsh extending 4 ha over saturated soil, interspersed with shallow pools of standing water.

Species identifications were made based on Pilsbry's material in The Academy of Natural Sciences collected in 1905 (Table 1). Localities 1-4 are called Falls, Watercress, Fenner, and Sullivan, respectively, in Table 1 and text to follow. Specimens were re-collected for anatomical and electrophoretic studies at the Chittenango Falls site in October, 1984, and August, 1985, by A. Breisch. One of us (Hoagland) visited the site for ecological observations in September, 1984.

Specimens of two shell types A and B, thought to be similar to *Succinea o. chittenangoensis,* were collected by T. Frest in Minnesota and sent to our laboratory for electrophoresis. The localities are described in Table 2.

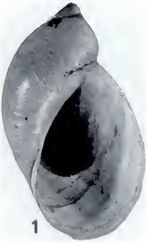
We failed to collect *Succinea ovalis* at the type locality, Philadelphia, in 1984, 1985, and 1986. We did find a succineid living at the sides of a waterfall at the covered bridge, Thomas Mill Road, on Wissahickon Creek in the upper part of Fairmont Park, Philadelphia, in all three years. Its similarity to some of the specimens at Chittenango Falls caused us to include it in the study. Specimens of *S. ovalis* were obtained from the alcohol collections of The Academy of Natural Sciences of Philadelphia (A.N.S.P). Specimens of *S. putris* (Linnaeus) in alcohol were obtained from the Rijksmuseum, Leiden. Localities and catalog numbers of these specimens are in Table 2. All of the taxa examined electrophoretically

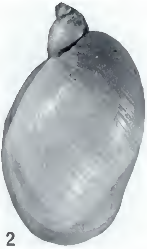
Table 2. Localities and catalog numbers of *Succinea* specimens compared with material from Chittenango Falls.

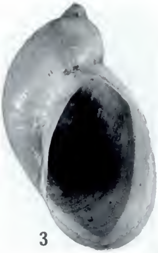
Taxon	Locality	Number Electro- phoresed	Year Collected	ANSP Cat. No.
Novisuccinea sp. A				
Minnesota A	Deer Creek, Fillmore Co., MN	18	1984	361446; A1160
Minnesota B	Canfield Creek, Fillmore Co., MN	19	1984	361447; A116611
S. sp. C	Wissahickon Creek, Fairmont Park	26	1984-5	A11612
S. cf. *putris*	Overijssel, Ommen, along the Vecht The Netherlands	0*	1968	no number; Rijksmuseum, Leiden
N. ovalis	Above Edgewater Park, near Delaware River, Burlington Co., NJ	0*	1908	95870; A9759
N. ovalis	Cazenovia, Madison Co., NY	0*	1905	90111; 4158
N. ovalis	Wissahickon Creek, Fairmont Park Thomas Mill Rd. Bridge, Phila., PA	0*	1923	46566; A9758D
N. chittenangoensis	Chittenango Falls, NY	0*	1905	90095; A4117 PARATYPES

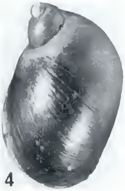
* Alcohol specimens only

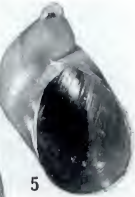
FIGS. 1-15: Scale Bar = 0.5 mm. **1-3,** *Succinea ovalis* Say, type specimens. Philadelphia, PA (ANSP 12390), three specimens. **4-5,** *Novisuccinea ovalis* Sullivan, New York, electrophoresed specimen (ANSP 358245). 4, ventral; 5, dorsal, same specimen. **6-7,** *Succinea ovalis chittenangoensis.* Pilsbry, holotype, Chittenango Falls, New York (ANSP 90087). 6, ventral; 7, dorsal. **8-9,** *Novisuccinea chittenangoensis,* Lower Chittenango Falls, New York, electrophoresed specimen (ANSP 358243). 8, ventral; 9, dorsal, same specimen. **10-11,** *Succinea ovalis pleistocenica* Baker, paratype, three miles SW of Marshall, Clark County, IL (ANSP 142710). 10, 11, ventral and dorsal of same specimen. **12-13,** *Succinea* sp. A, Fillmore County, Minnesota Type B (ANSP 361447). 14, ventral; 15, dorsal, two electrophoresed specimens, 18.7 mm and 15.7 mm in height. **14-15,** *Succinea* sp. A, Fillmore County, Minnesota Type B (ANSP 361447). 14, ventral; 15, dorsal, two electrophoresed specimens, 18.7 mm and 15.7 mm in height.

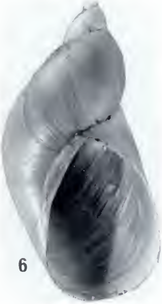

1

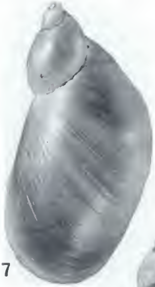

2

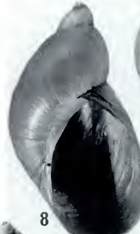

3

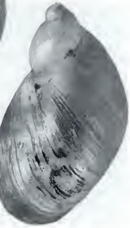

4

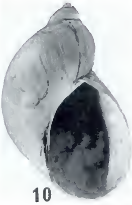

5

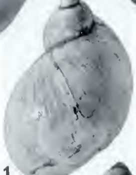

6

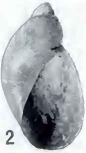

7

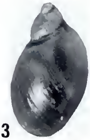

8

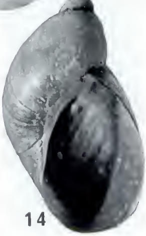

9

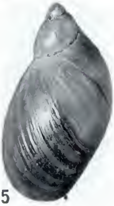

10


11


12


13


14


15

5 mm

and anatomically, together with type specimens of several of the key taxa, are illustrated in Figures 1-35.

TAXA TREATED

	Anatomy	Electrophoresis
Oxyloma Westerlund		
O. decampi gouldi Pilsbry 1948	-	+
O. retusa (Lea 1834)	-	+
Fenner population		
Sullivan population		
Novisuccinea Pilsbry		
N. chittenangoensis (Pilsbry 1948)	+	+
N. ovalis (Say 1817)	+	+
N. sp. A	+	+
population Minn. A		
population Minn. B		
Succinea Draparnaud		
S. cf. *pennsylvanica* Pilsbry 1948 (=H_1 ; watercress)	+	+
Succinea putris complex		
S. cf. *putris* (Linnaeus)	+	-
S. sp B. (= H_2; Falls, Watercress)	+	+
Falls population		
Watercress population		
S. sp. C (=Wissahickon)	+	+

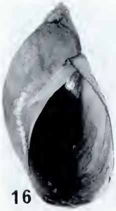
HABITATS

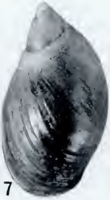
Novisuccinea chittenangoensis was found alive on weedy plants and talus in shade at the east side of the lower falls at Chittenango State Park living in sympatry with *Oxyloma retusa*, *O. decampi gouldi*, and *Succinea* sp. B. Specimens of *N. chittenangoensis* were found both on tall weeds and on the ground in wet, decomposing leaf litter. No specimens were found in the flowing water of the falls, but a few were on rock seepages. No specimens of *S.* sp. B were found on bare rock. Some specimens of *N. chittenangoensis* were on vegetation covering talus on a ledge to the side just above the base of the falls. Some had formed epiphragms and were found inside curled, dry leaves. *O. decampi gouldi* was restricted to green vegetation.

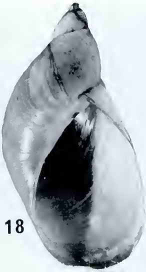
Fossil and/or subfossil shells of *Novisuccinea chittenangoensis* were abundant in dirt cliffs on the west side below the base of the falls. The fossils were on the average larger than the living shells.

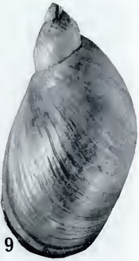
A few yards below the falls in a weedy area with watercress and other plants were *Succinea* sp. B and *S.* cf. *pennsylvanica* in addition to *Oxyloma retusa*, but no *N. chittenangoensis*. *Oxyloma retusa* tended to occupy lower levels of vegetation than the *Succinea*. Some specimens of O. *retusa* were crawling on damp leaf litter. The *Succinea* sp. B and *S.* cf. *pennsylvanica* were often found hanging upside-down secured by an

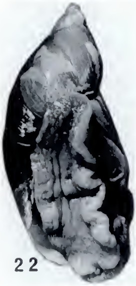
FIGS. 16-31. Scale bar = 0.3 mm for Figs. 26, 27, 32, and 33. Scale bar = 0.5 mm for all others. **16-17,** *Succinea* cf. *pennsylvanica*, Chittenango Falls, New York, Watercress beds, electrophoresed specimen (ANSP A11609A). 16, 17, ventral and dorsal of same specimen. **18-19,** *Succinea* sp. B, Chittenango Falls, New York, lower falls, electrophoresed specimen (ANSP 358244). 18, 19, ventral and dorsal of same specimen. **20-21,** *Succinea* sp. C, Wissahickon Creek, Chestnut Hill, PA (ANSP A11612). 20, ventral; 21, dorsal, two electrophoresed specimens, 17.7 mm and 14.7 mm in height. **22-23,** *Succinea putris* (Linnaeus), Noord-Brabant, Biesbosch, Netherlands, Aug. 3, 1958, C. O. van Regteren Altena, Coll. Rijksmuseum van Natuurlijke, Leiden. 22, ventral; 23, dorsal, two specimens, 20.5 mm and 19.6 mm in height. **24-25,** *Succinea pennsylvanica* Pilsbry, paratypes. Derrick City, PA (ANSP 142496). 24, ventral; 25, dorsal, two specimens, 16.8 mm and 15.2 mm in height. **26-29,** *Oxyloma decampi* (Tryon), holotype, Marshall, MI (ANSP 142710). 26-27, ventral and dorsal of same specimen, 3x. 28-29, ventral and dorsal of same specimen, 5x. **30-31,** *Oxyloma decampi gouldi* Pilsbry, Chittenango Falls, lower falls, electrophoresed specimen (ANSP 358240). 30, 31, ventral and dorsal of same specimen. **32-35,** *Oxyloma retusa* (Lea). Sullivan, New York. Electrophoresed specimen (ANSP 358246). 32-33, ventral and dorsal, 3x. 34-35, ventral and dorsal, 5x.

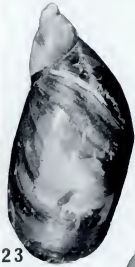

16

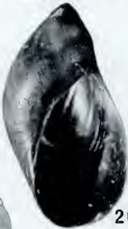

17

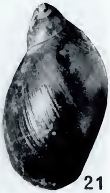

18

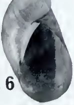

19

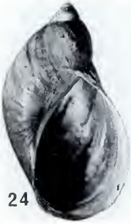

22

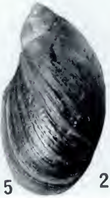

23

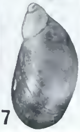

20

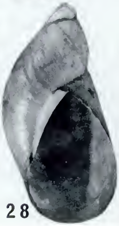

21

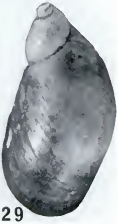

26

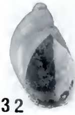

24

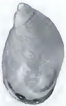

25

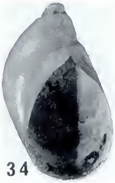

27

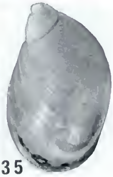

28

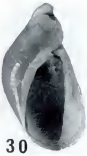

29


32


33


34


35


30

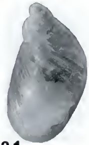

31

Table 3. Riexinger's microgeographic locality data, tentative species identification, and species determination by Hoagland for succineid snail specimens collected in 1983.

Sample	Tentative ID	Hoagland ID	Collection Site*	Characteristics
A	*S. ovalis*	*O. retusa*	Site 1	all sizes
B	*S. ovalis*	*N. ovalis,* *O. retusa*	Site 2	large and medium
C	*S. ovalis*	*O. retusa*	Site 2	medium and small
D	*S. chittenangoensis*	*S. sp. B,* *N. chit.,* *O. retusa*	Lower Falls	12 dark morph, 5 light morph, 1 amber
E	*S. chittenangoensis*	*S. sp. B*	Upper Falls	15 medium light morph
F	*S. ovalis*	*N. ovalis*	Site 2	all large
G	*S. chittenangoensis*	*S. sp. B*	Watercress	10 large light morph
H	*S. chittenangoensis*	*S. sp. B*	Watercress	10 large light morph
I	*S. chittenangoensis*	*S. sp. B*	Watercress	16 medium light morph
J	*Oxyloma sp.*	*O. d. gouldi*	Lower Falls	11 small to medium

*For details see locality data.

epiphragm inside curled, dry leaves. In daylight, specimens were both active and quiescent on *Angelica atropurpurea* and other tall weeds growing beside Chittenango Creek. The snails were observed consuming leaves from these plants.

Succinea sp. B and *S.* cf. *pennsylvanica* were found on the ground on damp, rotting leaf litter and wood, where egg masses were also found. Twenty-five meters below the falls beside the stream was a marshy area with a spring, covered in water cress, forget-me-nots, and mint as well as other low vegetation. This area contained *Succinea* sp. B, and possibly *S.* cf. *pennsylvanica*, laying eggs. In early September, 1984, egg masses and young snails were very common in marshy areas below the falls, but were less common in the direct spray zone at the side adjacent to the lower face of the falls.

The two habitats at and below the waterfall were quite different; the former is characterized by dampness due to spray from the falls, although drying can occur in autumn when water flow and wind are low. The latter varies from marshy to dry, depending on the volume of water in the spring and in the stream below the falls. The vegetation is probably not stable in composition from year to year.

Ecological field and laboratory studies of *Novisuccinea chittenangoensis* and the other succineid taxa were performed by Aloi and Ringler (1982), Aloi (1985) and Thomée and Dindal (1984). We will not give detailed ecological data here. We do caution that there was confusion over the identity of *N. chittenangoensis* in these works and in Riexinger et al. (1983), Aloi (1985) and Thomée (1986). *Novisuccinea chittenangoensis* was confounded with *Succinea* sp. B and *S.* cf. *pennsylvanica* (see Discussion). *Succinea* sp. B and *S.* cf. *pennsylvanica* were not distinguished from each other in the studies. Juvenile *Succinea* spp. are difficult to distinguish from *Oxyloma*, and probably were confused. For example, Table 3 lists the 10 samples first sent to us for electrophoresis, their tentative identification by Riexinger, and our identifications based on shell shape (comparisons with type specimens) and electrophoresis.

Novisuccinea ovalis was found in the vicinity of Chittenango Falls, but not at the Falls itself, and not in sympatry with *N. chittenangoensis*. We do not know the abundance of *N. ovalis* at the Sullivan site, but Hoagland and Breisch could find only *O. retusa* there in September, 1984. In September, 1984, *Succinea* sp. B was by far the most abundant species at the watercress sites, while *N. chittenangoensis* was the most abundant on the Falls. Numerous half-grown specimens of *N. chittenangoensis* were present, but no eggs or hatchlings were observed. *Oxyloma retusa* had the greatest geographical distribution. Both *Novisuccinea chittenangoensis* and *O. decampi gouldi* were limited to a single habitat at a single site.

Riexinger collected succineids from several sites in New York State in a search for more populations of *N. chittenangoensis* but did not find any. Thomée (1986) tried to cross succineid snails from Allegheny State Park with *Succinea* sp. B from the Falls. Offspring were produced, but because of the ability of land snails to self-fertilize and probably to store sperm, we cannot be sure that cross-fertilization took place. The Allegheny specimens were of a shell type similar to *Succinea* cf. *pennsylvanica*, but larger than those found at Chittenango Falls.

Succinea sp. C from Wissahickon Creek, PA, was found in a habitat very similar to that of *N. chittenangoensis*, except the waterfall and creek were much smaller. The snails were living on weedy vegetation, including nettles, on one side of the falls in the spray zone. In our continued search for topotype material of *N. ovalis*, we located another population of *S.* sp. C in 1986. It was on Barbados Island in the Schuylkill River at Norristown, Pennsylvania. This site is near the first; Wissahickon Creek drains into the Schuylkill River at a site below Norristown. The population of *Succinea* on Barbados Island was very large during early summer. Snails were found on weeds at the upstream end of the island. The snails were active on living vegetation and in leaf litter even when it had not rained for over a week; the ground was not swampy.

We have not visited field sites for the Minnesota specimens of *Succinea* sp. A, but Frest (pers. comm.) described the sites as talus similar to that at Chittenango Falls.

METHODS

General

Specimens from each locality in the Chittenango Falls and the Minnesota areas were roughly sorted by shell type and sent alive to The Academy of Natural Sciences of Philadelphia, where they were frozen, still in the shells, in tris tissue buffer. Several specimens of each shell type were drowned, then fixed in 4% formalin and preserved in 70% alcohol as voucher specimens and for anatomical studies. The vouchers are deposited in the malacological collections at The Academy of Natural Sciences.

Electrophoresis

Specimens to be electrophoresed were removed from the shells and the shells numbered and cataloged. All shell types from Chittenango Falls were represented on a single gel so that their electrophoretic patterns could be compared directly. Similarly, specimens from Minnesota and Wissahickson were run together with two shell types from Chittenango Falls, including *Novisuccinea chittenangoensis*. Whole specimens were ground after washing in distilled water to remove excess mucus.

Horizontal starch-gel electrophoresis was carried out, followed by staining for 19 specific enzymes. The general methods of Ayala et al.

Table 4. Conditions for Electrophoresis

Tris-Citrate pH 6, 2.5 hr., 35 MA
Acid phosphotase (AcPh) - 1*
Isocitrate dehydrogenase (IsDH); locus II-1
Leucine amino peptidase (LAP) -1

Tris-Citrate pH 6, 3.0 hr., 35 MA
Glucose-phosphate-isomerase (GPI) - 1
Malate dehydrogenase-NAD (MDH-NAD) - 2

Tris-EDTA-Borate (TEB), pH 8, 3.5 hr., 35 MA
Aldehyde oxidase (AO) - 1
*α*glycerophosphate dehydrogenase (*α*GPDH) locus II - 1
Hexokinase (Hex) - 2
Xanthine dehydrogenase (XDH) - 1

Poulik gel buffer pH 8.9, tray buffer pH 7.6, 3.0 hr., 35 MA
Esterase NA (EST) - 5
Peptidase/Glycine (Pep G) - 1
Peptidase/Tyrosine (Pep T) - 3
*α*GPDH locus I - 1

Tris-EDTA-Borate, pH 9.1, 4.5 hr., 350 V
Aspartate amino transferase (AAT) - 2
Glucose 3-phosphate dehydrogenase (G3PDH) - 1
Mannose-6 phosphate isomerase (MPI) - 1
Sorbitol dehydrogenase (SoDH) - 1

TEB gel buffer pH 9.1, tray buffer pH 8, 2 hr., 35 MA
Glucose 6-phosphate dehydrogenase (G6PDH) - 1
Phosphoglucomutase (PGM) - 2
6-phosphogluconate dehydrogenase (6PGDH) - 1
Superoxide dismutase (SOD) - 1

---

*Number of loci resolved per enzyme system.

(1973) as amended by Dillon & Davis (1980) and Davis et al. (1981) were applied to these mollusks. Starch gels (13%) were prepared using 33.5 g of Electrostarch and 250 ml of one of four gel buffers: (1) tris citrate, pH 6.0; (2) tris citrate pH 8.75 gel buffer & sodium borate, pH 7.6 tray buffer; (3) tris-EDTA-borate (TEB), pH 8.0; and (4) TEB, pH 9.1. Five enzyme systems were run on TEB of pH 9.1 but with tray buffer of pH 8. Table 4 reports the gel and tray buffers, current, and run time for each of the enzymes.

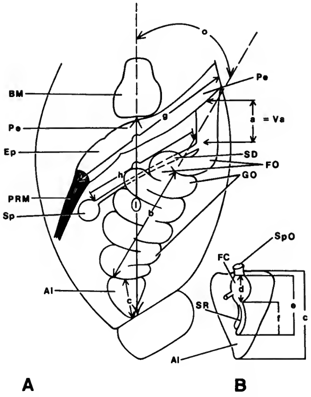


FIG. 36. Schematic drawing showing the positional relationships among organs within the body of succineids of this study seen in dorsal dissection. See pg. 26 for key to the abbreviations. A, dorsal aspect of the body showing only the body whorl and penultimate whorl. B, albumen gland enlarged and showing the ventral side. In A, the angle shown is that of the direction of coiling of the oviduct relative to the line drawn through the center of the body. **a.** length of vagina; **b.** length of glandular oviduct; **c.** length of albumen gland; **d.** length of fertilization chamber; **e.** length of fertilization chamber and seminal receptacles; **f.** length of seminal receptacles; **g.** length of penis complex; **h.** length of the spermathecal duct; **i.** length of the body whorl (mid-body from posterior buccal mass to posterior dorsal body whorl wall.

Six wicks of No. 3 Whatman filter paper were saturated with homogenized tissue from each individual. They were blotted and applied, one wick from each individual, to each of six gels to be run concurrently. The gels were sliced into three or four slabs for staining, so all 19 enzyme systems could be examined in one day. Agar overlays (10 ml of a 2% solution) were employed for all enzyme assays except AAT, G3PDH, and LAP, for which aqueous solutions were used. Standard recipes for all systems are in Shaw & Prasad (1970), Brewer (1970), and Poulik (1957). Gels were scored as described in Ayala et al. (1973). First, independent loci were identified (Tracey et al. 1975). The alleles of each locus were identified by the distance, in mm, that they migrated with respect to the most common allele of a reference population, which was given the arbitrary number 100. The reference population was *Novisuccinea ovalis* from Sullivan, N.Y. The time period for each run of a particular enzyme was standardized (Table 4). Assignment of electrophoretic patterns to loci and consequent interpretations were made with the aid of data collected on the same enzyme systems for mollusks (Davis et al. 1981) and other organisms (Lewontin 1974). Heterozygote banding patterns corresponded with the subunit compositions of the enzymes.

Tables 1 and 2 show the number of specimens electrophoresed from each locality and of each shell type. Sample sizes are small because of the possibly-endangered nature of some species, namely *Novisuccinea chittenangoensis*. Data analysis was done using the BIO-SYS-1 program, release 1.5 (Swofford & Selander 1981). The program was modified to handle the 31 loci detected in this study; there were a total of 11 samples of 8 shell types. Data were input as genotypes.

Rogers's, Nei's, and Cavalli-Sforza & Edwards's measures of similarity and distance were calculated comparing all populations (Rogers 1972; Nei 1972, 1978; Cavalli-Sforza & Edwards 1967). Cluster analyses were performed based on the measures of similarity and distance, using the unweighted pair-group method of arithmetic averaging. The distance Wagner procedure with the tree rooted at the midpoint of the greatest patristic distance was also used to generate a phylogenetic tree with the Cavalli-Sforza & Edwards chord distance as the distance coefficient. This last procedure gave the highest cophenetic correlation.

Morphology

Shells. Shells of the electrophoresed specimens were examined and sorted according to shell characters prior to electrophoresis, then sorted in accord with the electrophoresed patterns afterwards. The shell phenotypes were described. Then, the specimens were compared with descriptions in the literature and specimens in the collections of The Academy of Natural Sciences, including type material of *Succinea (Novisuccinea) ovalis* Say, *Succinea ovalis (=Novisuccinea) chittenangoensis* Pilsbry, and *Succinea (Novissuccinea) ovalis pleistocenica* Baker. All Succineidae in the collections from New York, New Jersey, and Pennsylvania were examined, with attention to material identified by Pilsbry and particularly to that collected by him in 1905 in the Chittenango area. The shell collections of Succineidae at the Academy were examined for material approximating the shell form of *S. o. chittenangoensis*, regardless of locality.

Each taxon is treated in turn; summaries of shell data (Table 5) and anatomical characters are provided. The simplicity of the succineid shell provides few independent characters of taxonomic importance. All species are within the shape range of ovate-conic to ovate-turreted. Microsculpture and columellar teeth are absent. Major shell characters separating the taxa are the length, width, and number of whorls in mature specimens, the relative lengths of spire, body whorl, and aperture, the depth of the suture separating the whorls (and hence the roundness of the whorls), the degree of inflation of the body whorl (hence the width of the body whorl for a given shell length), the shoulder angle, and the apical angle. Shell colors are subtle and might be site-specific for a particular species; they do not always match older museum shells from the same

Table 5A. Summary of shell and body color data for eight populations of succineid land snails used in this study.

	Character states	*N. ovalis*	*N. chitt.*	*N. sp. A* Minn. A	*N. sp. A* Minn. B	*S. putris*	*S. cf. penn.*	*S. sp. B*	*S. sp. C*
1	Maximum number of whorls	3	3.5	3.2	3.25	3.5	2.75 (juveniles?)	3.5	3.25
2	Shoulder shape O, flat; to 3, round. Mean/score	0.18/2	0.32/3	0.22/2	0.23/2	0.10/0	0.10/0	0.15/1	0.09/0
3	Relative spire height (L. spire/total L.) Mean/relative score	0.34/0	0.44/2	0.41/2	0.43/2	0.43/2	0.36/1	0.38/1	0.31/0
4	Shell thickness O, thin; 2, thick (subjective opinion)	0	1	1	2	0?	1	1	1
5	Inflation of body whorl = W:L. O=low; 2 = high. Mean/score	0.60/2	0.54/1	0.54/1	0.54/1	0.49/0	0.57/2	0.53/1	0.55/1
6	Maxiumu L. max/mean (O = short; 2 = tall)	15.6/15.0 1	20.5/18.3 2	10.8/10.6 0	16.2/15.4 1	19.8/18.8 2	9.6/9.6 0	19.2/17 2	19.8/18.8 2
7	Spire Angle. Angle/score	65/1	66/1	55/0	64/1	63/1	65/1	53/0	57/0
8	Translation: (L/No. whorls) O, small; 2, large. Ratio/score	4.9/1	5.5/2	3.5/0	4.9/1	5.5/2	3.7/0	5.3/2	4.9/1

Table 5B. Shell measurements (mm) taken from shells used for electrophoresis (except *S. putris*, which was not electrophorized). Mean ± standard deviation [Sn-1] (range). N = number measured.

	N. ovalis	*N. chitt*	*N. sp. A* Minn. A	*N. sp. A* Minn. B	*S. putris*	*S.* cf. *penn.*	*S. sp. B*	*S. sp. C*
1. Length (L.)	15.0 ± 0.6 (13.7-15.6) N=8	18.3 ± 1.6 (17.0-20.5) N=5	10.65 (10.5-10.8) N=2	15.9 ± 1.3 (14.8-16.2) N=4	18.8 ± 0.7 (18.0-19.8) N=4	9.6 —, N=2	17.0 ± 1.2 (15.7-19.2) N=8	14.5 ± 1.2 (13.4-16.8) N=7
2. Width (W.)	9.0 ± 0.4 (8.3-9.7) N=8	9.9 ± 0.5 (9.5-10.7) N=5	5.75 (5.5-6.0) N=2	8.6 ± 0.9 (7.8-9.5) N=4	9.2 ± 0.4 (8.8-9.7) N=4	5.5 (5.3-5.7) N=2	9.0 ± 0.6 (8.3-9.8) N=8	8.0 ± 0.4 7.7-8.3) N=7
3. L. aperture	10.9 ± 0.4 (10.0-11.3) N=8	11.5 ± 1.3 (10.3-13.0)N=5	6.85 (6.5-7.2) N=2	10.3 ± 1.0 (9.3-11.5) N=4	12.1 ± 0.8 (11.5-13.3)N=4	6.75 (6.7-6.8) N=2	11.2 ± 0.9 (10.2-12.5) N=8	10.4 ± 0.7 (9.7-11.7) N=7
4. L. spire	5.1 ± 0.5 (4.0-5.5) N=8	8.4 ± 0.5 (7.7-9.0) N=5	4.4 (4.3-4.5) N=2	6.9 ± 0.8 (6.3-8.0) N=3	8.1 ± 0.7 (7.5-9.0) N=4	3.5 —, N=2	6.5 ± 0.7 (5.5-7.5) N=8	4.5 ± 0.5 (3.8-5.3) N=7
5. W. aperture	7.0 ± 0.3 (6.5-7.5) N=8	7.1 ± 0.7 (6.5-8.0) N=5	4.1 (4.0-4.2) N=2	6.3 ± 0.5 (5.8-6.8) N=4	7.1 ± 0.4 (6.7-7.5) N=4	4.0 (3.8-4.2) N=2	6.8 ± 0.5 (6.2-7.7) N=8	5.9 ± 0.4 5.7-6.5) N=7
6. L. body whorl	13.8 ± 0.6 (12.5-14.3) N=8	16.3 ± 1.5 (15.0-18.2) N=5	9.5 (9.2-9.8) N=2	14.4 ± 1.2 (13.2-15.8) N=4	16.9 ± 1.0 (15.5-17.8) N=4	8.7 —, N=2	15.3 ± 0.8 (14.5-16.8) N=8	13.4 ± 1.1 (12.3-15.5) N=7
7. L. penultimate whorl	1.1 ± 0.2 (0.7-1.3) N=10	1.5 ± 0.2 (1.2-1.7) N=9	1.1 (0.9-1.25) N=2	1.2 ± 0.1 (1.0-1.3) N=4	1.5 ± 0.2 (1.2-1.7) N=4	0.8 —, N=2	1.3 ± 0.2 (1.0-1.5) N=8	0.75 ± 0.07 (0.6-0.8) N=12
8. W. penultimate whorl	2.1 ± 0.2 (2.0-2.5) N=10	2.9 ± 0.2 (2.8-3.2) N=9	1.9 (91.8-2.0) N=2	2.2 ± 0.4 (1.5-2.4) N=4	3.0 ± 0.3 (2.7-3.3) N=4	1.65 (1.6-1.7) N=2	2.6 ± 0.4 (2.2-3.2) N=8	1.9 ± 0.2 (1.6-2.3) N=12
9. L. 3rd. whorl	0.2 ± 0.1 (0.1-0.4) N=10	0.45 ± 0.1 (0.3-0.7) N=9	0.21 (0.17-0.25) N=2	0.4 ± 0.1 (0.3-0.45) N=4	0.68 ± 0.05 (0.6-0.7) N=4	0.1 —, N=2	0.5 ± 0.1 (0.3-0.7) N=3	0.17 ± 0.05 (0.1-0.2) N=12
10. W. 3rd whorl	0.6 ± 0.2 (0.3-0.9) N=10	1.1 ± 0.1 (1.0-1.2) N=9	0.6 (0.5-0.68) N=2	0.9 ± 0.1 (0.75-1.0) N=4	1.1 ± 0.1 (1.0-1.2) N=4	0.4 (0.3-0.5) N=2	0.9 ± 0.2 (0.7-1.3) N=8	0.45 ± 0.1 0.3-0.7) N=12
11. Spire angle (degrees)	65 ± 5 (60-72) N=10	66 ± 3 (60-70) N=9	55° (50-60) N=2	64 ± 3° (60-65) N=4	63 ± 3° (60-65) N=4	65 —, N=2	53 ± 2 (50-55) N=8	57 ± 2 (55-60) N=12
12. Aperture angle* (degrees)	80 ± 2 (75-83) N=10	64 ± 3 (60-70) N=9	58° (55-60) N=2	61 ± 5° (55-65) N=4	51 ± 3° (50-55) N=4	62 (60-65) N=2	58 ± 2 (56-62) N=8	69 ± 3 (60-72) N=12

*Place snail with aperture flat against glass slide surface; the angle is measured between the slide surface and the shell (from the adapical end of aperture). To measure, the snail must be fixed to the slide so that the slide can be tilted 90 degrees. Measurement is with an ocular angle-measurement disc mounted in the eyepiece of a dissecting microscope.

locality. Shell thickness appears to discriminate among the species but could have low heritability. We have tried to identify independent characters, both of shell and internal anatomy, in our taxonomic comparisons. Only living material was used to describe body color patterns, except for the published comments of Pilsbry (1948).

Illustrations of the shell phenotypes are in Figures 1-35.

Anatomy. In initiating anatomical studies of these succineid land snails, it became evident that reliable comparisons of intra- and interspecific differences among land snails call for a standardization of approach hitherto not seen among published land snail systematic work. Previously, anatomy has been presented, not as seen in the animal, but in artificial positions. In this regard there has not been much advance beyond Pilsbry (1948), who showed reproductive organs removed from the animal and pulled apart such that one cannot assess the correct positional relationships of those organs in the body of the animal or to each other. In the Pilsbry method the genital aperture is oriented towards the bottom of the page with the penial apparatus pulled to the left or right and remaining reproductive organ pulled to the other side. This is the system followed by Solem (1976) and others.

Patterson (1971) illustrated the reproductive system using a camera lucida. Again, however, the organs are shown removed from the body. How is the reader to know what the presentation of the organs is as if they were removed from a dorsal dissection and rotated 180 to show the ventral view?

In all works dealing with *Succinea*, as well as with other land snails, it is unclear what authors mean by short, medium, long (e.g., Patterson 1971). Few standards for quantification have been given, except the use of ratios such as length of vagina divided by length of penis (Franzen 1959) and vice-versa (Patterson 1971).

Methods used here are those employed by Davis (1967), Davis and Carney (1973), Davis et al. (1976), Davis and Greer (1980), and Davis et al. (1983) for prosobranchs but modified for succineids. The methods were developed to permit objective quantitative and qualitative intra-and interpopulation comparisons realizing that many important characters involve the positional relationships among organs and size-scaling factors. These often not-so-subtle characters are either not observed or are overlooked when the genital system is ripped out of the animal for study. What have previously passed for species-diagnostic characters really involved general organology which may or may not be species-specific.

The method used here is thus: (1) Present a primary illustration, in a standard orientation, of the organ systems as actually observed within the body, with key reference points clearly visible. (2) Subsequent illustrations are made with organs in the same positional relationship as in the primary illustration but with whole organs or parts of some organs removed to clarify underlying organs or connections of organs. Key reference points in the secondary illustration relate it to the exact positioning in the primary illustration. (3) In some instances an organ is rotated to show certain features. In such cases the direction and degree of rotation is shown. Again, key reference points relate to the primary illustration. Using these methods one can objectively determine inter- and intra-populational variation.

The standard orientation used here is dorsal, with dissections down through the thin dorsal wall. The shape of the body is shown to scale with the exact position of the reproductive system shown in relationship to the buccal mass, contour of the body whorl and subsequent whorls (Fig. 36). The only tissue removed to show this primary orientation is the mantle and thin enveloping connective tissue encasing the reproductive system. All other organs are ventral or ventrolateral to the reproductive system (e.g. esophagus, stomach, pericardium). It is within this context that Fig. 5 of Franzen (1959, p. 197) has substantive meaning in showing an essential difference between *S. ovalis* and a species from the *S. putris* complex used here for the schematic diagram in Fig. 36. In Fig. 36B the albumen gland is turned over 180° to show the interrelationships of the hermaproditic duct (HD) the fertilization chamber (FCh), seminal receptacles (SR) and spermoviduct (SpO).

Size scaling is accomplished using a series of measurements (Fig 36; Tables 6, 7) that are explained in the figure caption for Fig. 36. Some added explanation is essential here. The length of body (i) is, for the purposes of this paper, the distance from the posterior end of the buccal mass to the posterior end of the body whorl measured mid-body. There is little variance in this measure due to variance in procedures of relaxing and/or fixing the animal given animals of the same size shell. The length of penis (g) includes only the dorsal surface as illustrated, not any part that bends ventrally. This length usually includes the penis and epihallus. In no circumstance does it include the vas deferens. The length of the spermathecal duct (h) is the actual length following all folds and bends, not the direct distance from vagina to spermatheca. The angle shown (Fig. 36)is the angle of orientation of the glandular oviduct (b) to the mid-body line (i). The orientation of the glandular oviduct is determined by a straight line drown through the axis of coiling of the glandular oviduct as shown. There will be some error of measurement, approximately ±3°. This is not a problem as the trends examined for are large differences, not small scale differences (see Table 8). Organs are small, medium or long as defined by ranges of ratios.

Ratios used are as follows: (1) length of vagina/length of penis (Fig. 36; a/g); (2) length of vagina/length of spermathecal duct (Fig. 36; a/h); 3) length of seminal receptacles/length of seminal receptacles and length of fertilization chamber (Fig. 36; f/(d+f); (4) length of seminal receptacles/length of the albumen gland (Fig. 36; f/c); (5) length of albumen gland/length of glandular oviduct (Fig. 36; c/b); (6) length of glandular oviduct/length of body (Fig. 36; b/i); (7) length of albumen gland/length of body (Fig. 36; c/i); (8) length of penis/length of body (Fig. 36; g/i); (9) length of vagina/length of body (Fig. 36; a/i).

Disclaimer about ratio data: Nine ratios were used here to explore their use to assess the relative lengths of certain organs. These were chosen based on prior impressions about relative organ size while doing dissections. Some may be of use, others not. Those relationships clearly of use are to be used in a multivariate analysis to produce a phenogram showing relationships among the eight populations studied here. The ratios themselves will not be used in the multivariate analysis, rather binary scores will be used for organs small, medium or long as defined by ranges of ratios. Data of ratios are used provisionally as too few specimens were available for each population to adequately explore variance.

BASIC SUCCINEID ANATOMY

Morphological characters traditionally used to distinguish among species of *Succinea* have been those of shell, radula, jaw, body form, retractor muscles, and reproductive system (Quick 1933; Pilsbry 1948; Patterson 1971). The present study is limited in that the focus is on shell, reproductive system, and molecular genetics. The nature of the contract with the state of New York sponsoring this work coupled with the sparse material available precluded a full morphological study that would ideally have included nervous, muscular, and digestive systems.

Opening the animal dorsally one can readily discern the penis (Pe), the free oviduct (FO), and glandular oviduct (GO) as well as the albumen gland (Al) (Fig. 36). In fully mature (sexually) animals the glandular oviduct may be so swollen as to push anteriorly over the penis. In many cases a short section of vagina (Va) may be seen close to the penis, the rest being covered dorsally by the coils of the free oviduct.

Penial Complex (Proximal Penis, Distal Penis, Epiphallus). Both the penis and the vagina open directly at the genital aperture (Fig. 48, GA), with no intervening vestibule or atrium. In dorsal view the penis obliquely crosses the vagina such that the penial part of the genital aperture is dorsal to the vaginal part of the common

Table 6. Ratios examined for their value in discriminating among populations and species of succineids. Mean ± standard deviation; N = number used.

	S. cf. *penn.*	*S. sp. B*	*S. putr.*	*S. sp. C*	*N. oval*	*N. chit*	*N. Minn A*	*N. Minn B*
1. Length of vagina/ length of penis	0.13 ± 0.10 N=3	0.17 ± 0.10 N=4	0.15 ± 0.03 N=2	0.23 N=1	0.60 ± 0.08 N=3	0.37 ± 0.02 N=4	0.44 ± 0.08 N=2	0.57 ± 0.05 N=2
2. Length of vagina/ length of body	0.27 ± 0.05 N=3	0.14 ± 0.03 N=4	0.21 ± 0.04 N=3	0.15 ± 0.02 N=2	0.36 ± 0.06 N=3	0.21 ± 0.04 N=3	0.42 N=1	0.39 N=1
3. Length of vagina/ length of spermathecal duct	0.40 ± 0.16 N=3	0.43 ± 0.11 N=4	0.22 ± 0.08 N=3	0.32 ± 0.02 N=2	0.59 ± 0.07 N=4	0.54 ± 0.25 N=4	0.71 N=1	0.51 ± 0.04 N=2
4. Length of seminal receptacle/length of albumen gland	0.45 ± 0.08 N=3	0.93 ± 0.13 N=5	0.37 ± 0.06 N=3	0.43 ± 0.26 N=2	0.18 ± 0.04 N=3	0.32 ± 0.04 N=3	0.17 ± 0.07 N=2	0.13 N=1
5. Length of seminal receptacle/lengths of fertilization chamber and seminal receptacle	0.54 ± 0.06 N=3	0.67 ± 0.04 N=3	0.61 ± 0.05 N=3	0.59 ± 0.13 N=2	NC	0.58 ± 0.03 N=4	0.53 N=1	0.50 N=1
6. Length of albumen gland/ length of glandular oviduct	0.27 N=1	0.52 ± 0.11 N=5	0.55 ± 0.04 N=2	0.60 ± 0.04 N=2	0.56 ± 0.32 N=4	0.45 ± 0.02 N=2	0.63 N=1	0.91 ± 0.20 N=2
7. Length of albumen gland/ length of body	0.13 ± 0.03 N=2	0.32 ± 0.04 N=5	0.27 ± 0.04 N=2	0.39 ± 0.07 N=2	0.23 ± 0.07 N=2	0.21 ± 0.05 N=2	0.28 N=1	0.42 ± 0.12 N=2
8. Length of glandular oviduct/length of body	0.60 ± 0.17 N=3	0.7 ± 0.10 N=5	0.56 ± 0.02 N=2	0.66 ± 0.16 N=2	0.23 ± 0.07 N=3	0.52 ± 0.10 N=3	0.46 N=1	0.49 ± 0.02 N=2
9. Length of penis/length of body	0.77 ± 0.18 N=3	0.62 ± 0.09 N=5	0.76 ± 0.02 N=2	0.73 ± 0.02 N=2	0.49 ± 0.12 N=3	0.52 ± 0.05 N=3	1.19 N=1	20.83 ± 0.01 N=2

Table 7. Organ sizes defined as long, medium or short based on data used to calculate ratios given in Table 5. Only ratios of discriminating potential are included. Numbers (column 1) refer to Table 6.

		Range	Means
1. Length of vagina /L. of penis:	short	0.12-0.27	(0.17; 0.15)
	medium	0.21-0.52	(0.31; 0.23; 0.37; 0.44)
	long	0.52-0.68	(0.57; 0.60)
2. Length of vagina /L of body:	short	0.10-0.20	(0.14; 0.15)
	medium	0.21-0.32	(0.21; 0.27)
	long	0.30-0.42	0.36; 0.39; 0.42)
3. Length of vagina/ L. of spermathecal duct:	short	0.14-0.30	(0.22)
	long	0.32-0.71	(0.32; 0.40; 0.43; 0.51; 0.54; 0.59; 0.71)
4. Length of seminal receptacle/ L. of albumen gland:	short	0.13-0.24	(0.13; 0.17; 0.18)
	long	0.26-0.53	(0.37; 0.32; 0.39; 0.43; 0.45)
6. Length of the albumen gland/ L. of glandular oviduct:	short	0.27	
	long	0.34-1.11	(0.45 to 0.91)
7. Length of the albumen gland / L. of body:	short	0.10-0.16	(0.13)
	medium	0.17-0.31	(0.21; 0.23; 0.27; 0.28
	long	0.32-0.54	(0.32; 0.39; 0.42)
8. Length of the glandular oviduct/ L. of body:	short	0.16-0.30	(0.23)short 0.16-0.30 (0.23)
	long	0.43-0.81	(0.46; 0.49; 0.52; 0.60; 0.66; 0.71)
9. Length of penis/L. of body:	short	0.37-0.61	(0.52; 0.49)
	medium	0.62-0.95	(0.62; 0.73; 0.77; 0.76; 0.83)
	long	1.19	

opening. This is not clear in a Pilsbry-style presentation (Pilsbry 1948; Solem 1976; Patterson 1971) but was clearly shown by Franzen (1959).

The penial complex consists of the penis proper, epiphallus, penis sheath and penial retractor muscle. The retracted (inverted) penis has a clearly defined proximal tube and distal section. Internal structures of the penis are seen by cutting the penis open along the dorsal surface using iridectomy scissors. The proximal tube has a thin wall with a number of elongated ridges and grooves. The lumen is large. The distal penis has a thickened wall, an internal coalescence of ridges that are highly folded thus appearing nodular, irregular grooves, and a narrow lumen. The structure traditionally called the epiphallus is highly variable but defined here as that section of tube distal to the penis s.s. that is considerably wider than the vas deferens and internally has a regular series of circular folds. Its lumen is wide. In some species, the three sections cannot be differentiated externally (Fig. 48); in others, the epiphallus is set off from the penis by a noticeable constriction (Fig. 44). In some species there is a constriction setting off the proximal penis from the distal penis, and the distal penis from the epiphallus (Fig. 45D). In some cases the penial tube becomes more slender at the epiphallus, and the epiphallus bends beneath the penis or bends around to run anteriorly beside the penis (Fig. 42).

In all species studied there is a penis sheath (PS). The sheath may enclose the entire penis and epiphallus (Fig. 52), or only a part of the penis-epiphallus tube (Figs. 42, 46). The penial retractor muscle (PRM) attaches at the posterior end of the sheath and runs to the dorsal postero-lateral body wall (Fig. 36).

Special comment must be made about the penis sheath. In *Novisuccinea* the sheath was always observed to terminate before the distal penis; the distal end of the sheath was never seen to be ripped or torn. In *Succinea* spp. B and C the sheath was always observed to enclose the entire penis including the epiphallus. In *Succinea* cf. *putris* the sheath always enclosed the entire penis but in some individuals the epiphallus bulged through and out of the sheath (Fig. 47B). However, it was clear that the sheath enclosed the distal end of the penis. In *Succinea* cf. *pennsylvanica* this character-state seemed in transition with the fundamental condition being as in *S.* cf. *putris*. In one case the condition appeared as in *Novisuccinea*. In other individuals the epiphallus had burst through the sheath and the sheath was clearly shattered; the retractor muscle and a bit of sheath were attached to the distal end of the epiphallus (as in all *Succinea* s.s.). In *Succinea* cf. *pennsylvanica* we interpret the fundamental condition to be as for all *Succiena* s.s., i.e. the sheath enclosed the entire penis (contrast *Novisuccinea*). The bursting through the sheath by the epiphallus probably has to do with copulations, less likely due to preservation artifact. In some few individuals the sheath does not, in development, fully encase the penis, hence this character-state is possibly in transition, i.e. is not fixed. In examining the series of individuals of *S.* cf. *pennsylvanica* it is clear that the fundamental condition is one seen in *Succinea*, not *Novisuccinea*. However, the various conditions are scored in Table 8 to reflect the actual conditions observed realizing that the bursting of the sheath may be an artifact, but also understanding that it may reflect a real condition that occurs in this species during copulation but not occuring in other species where the sheath encases the entire penis.

Vas Deferens-Prostate Complex. The vas deferens (VD) runs from the epiphallus to the prostate and then posteriorly to the spermoviduct (Fig. 42B). The vas deferens of all species studied runs from the epiphallus to the vagina coiled posterior to, ventral to, or antero-ventral to the penis; the vas deferens passes ventral to the right cephalic retractor muscle branching off the right tentacle retractor muscle (Fig. 37). The vas deferens then turns posteriorly to run to the prostate, passing ventral to the spermathecal duct (Fig. 39A). At the prostate the vas deferens may in some species swell considerably to form the ampulla of the vas deferens (Fig. 52 AmV).

There are species-specific characters involving the vas deferens. It may run from epiphallus to prostate as a circular tube highly muscularized with circular muscles, or as a flaccid tube with weak longitudinal muscles. It may run part way as a muscular circular tube and then abruptly change (ventral to the free oviduct) to a flattened unmuscularized tube (Fig. 40B).

The prostate varies in size and shape among species. It is located ventro-lateral to the mid-glandular oviduct (Figs. 41, 44). In some individuals part of the prostate is seen lateral to the mid glandular oviduct (Fig. 52). The prostate is brownish in preserved specimens and the surface is nodular. In some species the posterior prostate touches or is pressed against the albumen gland (Fig. 40C); in others these organs do not touch (Fig. 48). The vas deferens runs along a groove in the prostate. The vas deferens-prostate connection is along this groove. The grooved surface of prostate is directly ventral to the glan-

Table 8. Characters and character-states of value in distinguishing among species and populations of *Succinea* sensu lato.

---

1. Spermathecal duct massive at junction with the vagina and continues as a wide tube for about 1/2 its length (0,1).
2. Distal penis with a posterior blind sac (0,1).
3. Epiphallus begins as a slender duct arising about mid-distal penis and pressed against and bound to the distal penis (0,1).
4. Posterior prostate rests on anterior end of albumen gland or overlaps anterior ventral surface of the albumen gland (0,1).
5. Free oviduct wraps 360° around the spermathecal duct (0,1).
6. The penis sheath encases only the proximal and part of the distal penis (0,1)
7. A section of the vas deferens may be enclosed by the penis sheath with the loop of the epiphallus and section of vas deferens posterior to the penis sheath (i.e. free of the sheath).
8. The vas deferens makes a twist or coil at mid-length ventral to the free oviduct (0,1).
9. The penis sheath encases the entire penial complex (including the epiphallus) (0,1).
10. The epiphallus of some individuals may burst through part or the entire penis sheath covering the epiphallus (0,1).
11. The penis sheath may encase the proximal and entire distal penis but not the epiphallus (0,1).
12. The penial retractor muscle of some individuals attaches to the penis sheath at the posterior end of the epiphallus and again, after a short distance, to the loop of the vas deferens posterior to the penis (0,1).
13. The penial retractor muscle of some individuals attaches to the penis sheath as in 6 above, and also to the loop of the vas deferens (Fig. 43B) (0,1).
14. The spermathecal duct of some individuals is massive at the junction with the vagina, then quickly tapers to a narrow tube (Fig. 47B) (0,1).
15. The body is globose (0) or elongate (1).
16. Penis with very distinct epiphallus as seen from external view (Figs. 45D). (0,1)
17. Distal penis with an internal fleshy pad (Fig. 46G) (0,1).
18. Posterior end of prostate overlaps the ventral surface of the albumen gland for about 1/3 to 1/4th the length of the albumen gland (0,1)
19. The free oviduct is a direct continuation of the vagina (0), or arises from the right ventro-lateral side or ventral side of the vagina (1).
20. Vas deferens with pronounced circular musclar sheath throughout (0,1).
21. Vas deferens with weak longitudinal muscular sheath throughout (0,1).
22. Vas deferens from epiphallus to mid-vas deferens circular with circular muscles; posterior half a flattened ellipse and non muscular.
23. Posterior vas deferens pigmented (0,1).
24. Posterior vas deferens fused to the spermathecal duct by dense connective tissue (0,1).
25. Fertilization chamber and talons not pigmented (0,1).
26. Fertilization chamber and talons lightly pigmented (0,1)
27. Fertilization chamber and talons heavily pigmented (0,1).
28. From external view there appears to be only one seminal receptacle (0,1).
29. Vas deferens widens considerably at the anterior prostate to form the ampulla of prostate (0,1).
30. The angle of the glandular oviduct to the mid-line of the body is 0 to 30 degrees (0,1).
31. The angle above (No. 30) is 35 to 40 degrees (0,1).
32. The angle above (No. 30) is > 45 degrees (0,1).
33. The distal penis ends directly posterior to the

buccal mass or very close to that position (0,1).
34. Length of vagina/length of penis: short (0,1) (see p.479 for definition).*
35. Length of vagina/length of penis: medium (0,1).*
36. Length of vagina/length of penis: long (0,1).*
37. Length of vagina/length of body: short (0,1).*
38. Length of vagina/length of body: medium (0,1).*
39. Length of vagina/length of body: long (0,1).
40. Length of vagina/length of spermathecal duct: short (0); long (1).
41. Length of seminal receptacles/length of albumen gland: short (0); long (1).*
42. Length of albumen gland/length of glandular oviduct: short (0); long (1).*
43. Length of albumen gland/length of body: short (0,1).*
44. Length of albumen gland/length of body: meduim (0,1).*
45. Length of albumen gland/length of body: long (0,1).*
46. Length of glandular oviduct/length of body: short (0,1).*
47. Length of penis/length of body: short (0,1).*
48. Length of penis/length of body: medium (0,1).*
49. Length of penis/length of body: long (0,1).
50. Pronounced perireceptacular sac present (0,1).
51. Proximal penis has pronounced dilation at the proximal end (0,1).

---

dular oviduct in some species or ventro-lateral to the glandular oviduct in other species.

Female and Hermaphroditic Tracts. The vagina (Va) is that wide tube between the genital aperture and the point where the spermathecal duct (SD) branches off (Va, Fig. 36). The spermathecal duct runs dorsal to the vas deferens and ventral to the oviduct (free and glandular) (Fig. 37) to the spermatheca (Sp), a sac-like organ located to the left of the glandular oviduct, just posterior to the penis complex, and ventral to the penial retractor muscle (Fig. 37). The part of the spermathecal duct joining the oviduct at the vagina may, in some species, be a very wide duct (Fig. 37); in others, a slender duct (Fig. 46).

The oviduct begins at that point where the spermathecal duct branches off the vagina. There is a free portion and a glandular portion. The free portion contains coils that are readily separated. In some species the free oviduct coils 360° around the spermathecal duct (Fig. 39A). The glandular oviduct is a greatly convoluted tube from which swell numerous glandular lobes. In some species, when fully sexually mature, the glandular oviduct may nearly fill the entire dorsal aspect of the body whorl posterior to the buccal mass. The glandular oviduct becomes the spermoviduct at that point where the vas deferens joins it (slightly anterior to the albumen gland) and runs posteriorly into the fertilization chamber. The tube is called the spermoviduct as both sperm and eggs traverse this section of duct.

Swollen or not, the direction of coiling of the oviduct is a species-specific character. The midline of the glandular oviduct (b, Fig. 36) may vary between 0° and nearly 90° to the mid-line of the body.

The albumen gland is somewhat triangular and located immediately distal to the oviduct. The relative size of the organ is a species-specific character. The distal tip of the organ may twist partially into the penultimate whorl. The albumen gland is turned over 180° to show the ventral side and the organs located there, namely the seminal receptacles, fertilization chamber, and spermoviduct (Fig. 36B). The spermoviduct swells to form a fertilization chamber. The hermaphroditic duct (HD) attaches to the right side of the fertilization chamber as a slender tube (Fig. 37). The hermaphroditic duct may be greatly swollen in sexually mature animals; this duct transports sperm and oocytes from the gonad to

Table 9. Binary coding for presence (1) or absence (0) of 51 character-states given in Table 8 with ratios and sizes defined in Tables 6 and 7.

Char.	*S.* cf. *penn.*	*S.* sp. B	*S. putr*	*S. sp. C*	*N. oval*	*N. chit*	*N.* Minn A	*N.* Minn B
1	0	0	0	0	1	1	1	1
2	0	0	0	0	1	1	1	1
3	0	0	0	0	1	1	1	1
4	0	0	0	0	1	1	1	1
5	0	0	0	0	1	1	1	1
6	0	0	0	0	1	1	1	1
7	0	0	0	0	1	1	1	1
8	0	0	0	0	1	1	1	1
9	0	1	1	1	0	0	0	0
10	1	0	1	0	0	0	0	0
11	1	0		0	0	0	0	0
12	1	1	0	0	0	0	0	0
13	0	0	0	0	1	1	1	1
14	0	0	1	0	0	0	0	0
15	0	1	1	1	0	1	1	1
16	1	0	0	0	1	1	1	1
17	1	0	0	0	0	0	0	0
18	0	0	0	0	1	0	1	1
19	0	0	0	0	1	0	0	0
20	1	0	1	0	0	0	0	0
21	0	1	0	0	0	0	0	0
22	0	0	0	1	1	1	1	1
23	0	0	0	0	0	0	1	0
24	0	0	0	0	0	0	1	0
25	0	0	0	1	1	0	0	0
26	1	1	0	0	0	0	0	0
27	0	0	1	0	0	1	1	1
28	0	0	0	0	0	1	0	0
29	0	1	1	1	0	0	0	0
30	0	1	1	0	1	1	1	1
31	0	0	0	1	0	0	0	0
32	1	0	0	0	0	0	0	0
33	0	0	0	0	1	0	1	1
34	0	1	1	0	0	0	0	0
35	1	0	0	1	0	1	1	0
36	0	0	0	0	1	0	0	1
37	0	1	1	1	0	0	0	0
38	1	0	0	0	0	1	0	0
39	0	0	0	0	1	0	1	1
40	1	0	1	1	1	1	1	1
41	1	1	1	1	0	1	0	0
42	0	1	1	1	1	1	1	1
43	1	0	0	0	0	0	0	0
44	0	0	1	0	1	1	1	0
45	0	1	0	1	0	0	0	1
46	1	1	1	1	0	1	1	1
47	0	0	0	0	1	1	0	0
48	1	1	1	1	0	0	0	1
49	0	0	0	0	0	0	1	0
50	0	1	0	0	0	0	0	0
51	0	1	1	0	0	0	0	0

the fertilization chamber. The distal part of the hermaphroditic duct may extend into the penultimate whorl. The two seminal receptacles arise from the posterior end of the fertilization chamber. There are species-specific size differences. In some species the receptacles are so wrapped in connective tissue as to appear to be only a single organ. Species also differ in the degree to which the fertilization chamber, seminal receptacles, and hermaphroditic duct are pigmented with melanin.

In one species studied there was a pronounced flattened sac pressed about the seminal receptacles; the sac attached to and opened into the posterior end of the fertilization chamber. This we call the perireceptacular sac (PRS, Fig. 51, E-G). In some species the fertilization chamber extends somewhat posterior to the point where the seminal receptacles arise. This posterior portion has been called the fecundation pouch (Patterson 1971). Whether or not the perireceptacular sac and fecundation pouch are homologous has yet to be determined. In this study the perireceptacular sac is much larger than the posterior projection of the fertilization chamber.

Multivariate Analysis

In Table 8 are listed 51 character-states used in the multivariate analysis of anatomical data. All character-states are scored in binary fashion (0,1). The program NT-SYS was used (Rohlf et al.1972), with UPGMA, similarity and distance coefficients, phenograms, cophenetic correlations, and the minimum spanning tree. The rectangular matrix of OTUs and character-state scoring is given in Table 9.

Abbreviations used with the anatomical figures are defined below:

AFC	anterior fertilization chamber
Al	albumen gland
AmV	ampulla of the vas deferens
BM	buccal mass
DAL	duct albumen gland
Di	digestive gland
DP	distal penis
DPS	distal penial sac
Ep	epiphallus
Es	esophagus
FCh	fertilization chamber
FO	free oviduct
GA	genital aperture
GO	glandular oviduct
Gr	grooves
HD	hermaphroditic duct
J	jaw
Pe	penis
Pr	prostate
PrP	proximal penis
PRS	perireceptacular sac
PS	penis sheath
Ri	ridges
RCR	right cephalic retractor
RTR	right tentacular retractor mucle
SD	spermathecal duct
Sn	snout
Sp	spermatheca
Spo	spermoviduct
SR	seminal receptacle
Tn	tentacle
Va	vagina
VD	vas deferen

GENERIC DEFINITIONS

Based on the anatomical data there are two genera: *Succinea* Draparnaud 1801 and *Novisuccinea* Pilsbry 1948.

Novisuccinea Pilsbry 1948 was based on "typical species such as *S. ovalis* and *S. strigata.*" We here designate the type species as *S. ovalis* (Say 1817). The type locality is Philadelphia, Pa., U.S.A. The genus is defined on the following characters:

(1) The spermathecal duct is massive at the junction with the vagina and continues as a wide tube for about 1/2 the length of the spermathecal duct. (2) The free oviduct wraps 360° around the spermathecal duct. (3) The distal penis has a posterior blind sac. (4) The duct of the epiphallus arises from the distal penis anterior to the penis sac, as a slender duct that expands considerably and is pressed against the distal penis in a tight U-shaped bend. (5) The penis sheath encases only the proximal and part of the distal penis. (6) The

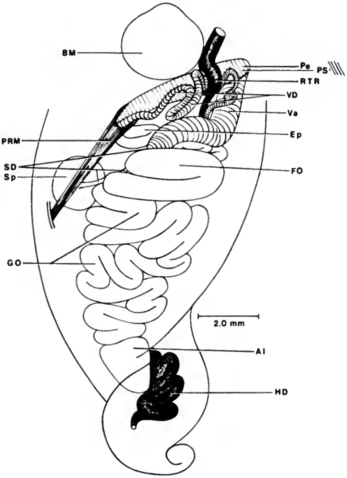


FIG. 37. *Novisuccinea chittenangoensis.*

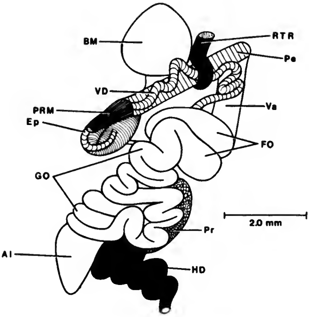


FIG. 38. *Novisuccinea chittenangoensis.* Variation where a portion of the prostate (Pr) is seen lateral to the glandular oviduct (GO); the epiphallus is twisted such that the narrow tubular proximal part of epiphallus is clearly seen (Ep).

penial retractor muscle of some individuals attaches not only to the penis sheath as positioned per 5 above but also to the loop of the vas deferens. (7) A section of the vas deferens may be enclosed by the penis sheath with part of the loop of the epiphallus. A section of the vas deferens is posterior to, and free of, the sheath. (8) The vas deferens makes a twist or coil at mid-length, i.e., at a position ventral to the free oviduct. (9) The posterior prostate rests on the anterior end of the albumen gland or overlaps the anterior ventral surface of the albumen gland.

Succinea has as type species *S. putris* (Linné). Pilsbry (1948) reviewed the designation of the type species. The type locality is northern Europe. The genus is defined on the basis of the following characters: (1) The spermathecal duct is slender at the vagina or, if massive, makes an abrupt transition to a slender tube close to the vagina. (2) The free oviduct does not make a 360° loop around the spermathecal duct. (3) The distal penis does not have a posterior blind sac. (4) The epiphallus arises directly from the distal end of the distal penis as a wide tube. (5) The penis sheath encases the entire penis and epiphallus. In one species the epiphallus may burst through the sheath; in another species the sheath may encase the entire penis but not the epiphallus. (6) In some individuals the penial retractor muscle attaches to the penis sheath at the distal end of the epiphallus and again, after a short distance, to the loop of the vas deferens posterior to the penis. (7) No part of the vas deferens is enclosed by the penis sheath. (8) The vas deferens does not make a twist or coil at mid-length. (9) The posterior end of the prostate does not reach or touch the albumen gland.

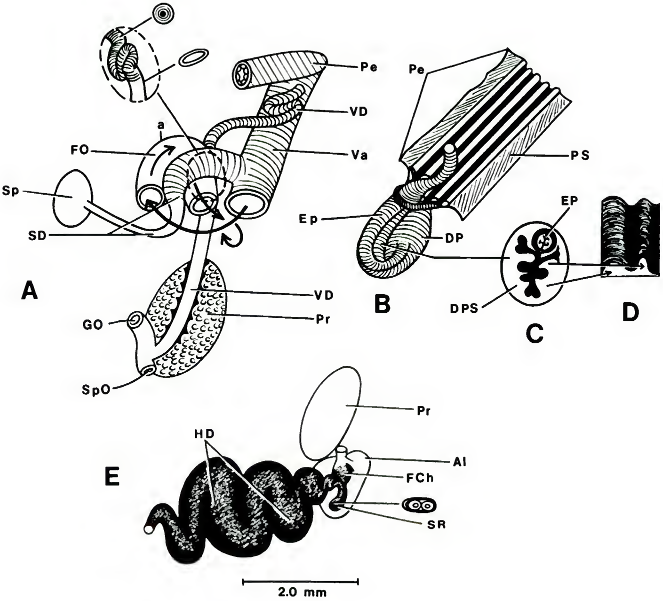


FIG. 39. *Novisuccinea chittenangoensis*. **A,** organs positioned as in Fig. 38 but with parts cut away to show the entire spermathecal duct (SD) and how the free oviduct coils 360 around the spermathecal duct. The dotted circle indicates the area ventral to the oviduct coil where the vas deferens (VD) coils at the point of transition from having a heavily muscular circular tube to a non-muscular flattened duct (see inset). **B,** penis in same position as in Fig. 38 with proximal penis slit open to show the elongated folds. This fig. shows that part of the epiphallus and vas deferens are within the penis sheath (PS). **C,** cross section to show the integrity of the narrow circular duct of the proximal epiphallus arising from the distal penis (DP). **D,** folds of the distal penis. **E,** albumen gland of Fig. 38 rotated 180 to show the finger-like seminal receptacle that, when cut across, reveals that there are the usual two seminal receptacles. The characteristic dense black pigmentation of the fertilization chamber and seminal receptacles is shown as well as the prostate (Pr) touching the albumen gland (Al).

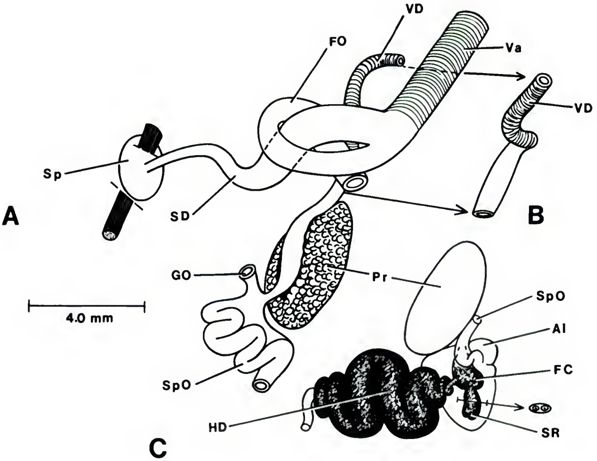


FIG. 40. *Novisuccinea chittenangoensis*. A, variation; the interrelationships of the vagina (Va), spermathecal duct (SD), spermatheca (Sp), vas deferens (VD) and prostate are shown. B, the coil in the vas deferens is shown. C, the ventral side of the albumen gland is shown. The blunt singular-looking seminal receptacles are slightly lobed at the distal end of the mass indicating the two separated seminal receptacles within.

Species Descriptions

NOVISUCCINEA

Novisuccinea chittenangoensis (Pilsbry 1908)
Succinea ovalis chittenangoensis Pilsbry 1908

SHELL. Large, elongate, with tall spire. Adults of 3.25 whorls. Shell suture deep; rounded sides of whorls. Shell of moderate thickness. Fresh shell grey-orange in color. Body whorl moderately expanded and lower lip of aperture flattened.

LIVING ANIMAL. First 1.5 whorls white or pinkish ("ruddy"; Pilsbry, 1948). Penultimate whorl yellow-olive or orange-pink with black splotches; a black band along the suture. First half of body whorl yellow or orange with strong black splotches forming a reticulate pattern as illustrated by Pilsbry (1948, p. 806). A strong sigmoid black band posterior to the kidney, which forms a dusky yellowish band. One white dot lies just posterior to the sigmoid band. Anterior to the kidney, there are black bands parallel to the suture which thicken and turn such that they meet the aperture at right angles. The ground color of this anterior portion of the body whorl is greenish yellow (or orange-yellow). The last half

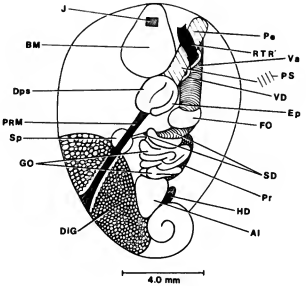


FIG. 41. *Novisuccinea ovalis*. Dorsal arrangement of organs relative to body and penulti-

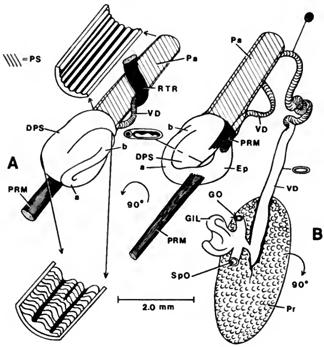


FIG. 42. *Novisuccinea ovalis*. Penis-epiphallus-prostate complex. **A**, penis positioned as in A. Insets show the longitudinal folds of the proximal penis and circular folds of the distal penis sac (DPS). **B**, the penis is rotated to show better the relationship of the distal penis sac (DPS) and the proximal origin of the epiphallus as well as how the distal end of the epiphallus and a section of the vas deferens (VD) run through the penis sheath. The coil of the vas deferens is shown at the region of transition from a muscular circular duct to

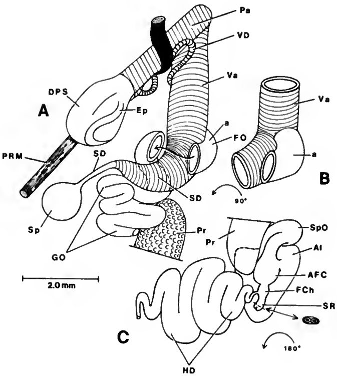


FIG. 43. *Novisuccinea ovalis*. **A**, entire spermathecal duct and how the oviduct encircles the spermathecal duct is shown. **B**, vagina was rotated to show where the free oviduct connects with the vagina. Point a in B is the same in A. **C**, ventral side of albumen gland showing prostate overlapping albumen gland, the lack of pigmentation on the fertilization chamber and the seminal receptacles.

of the body whorl also contains fine golden veins.

Foot light yellow with a discrete black spot on posterior dorsum. Black tentacles; black specked pigment on head. Dark band on sides of neck. Yellow pigment around genital pore.

ANATOMY. Diagnostic features are as follows (see Figs. 37-40): (1) The fertilization chamber and seminal receptacles are densely pigmented. (2) The body is elongated. (3) The free oviduct is a direct continuation of the vagina (Fig. 39A). (4) The length of the vagina relative to the length of the penis is medium. (5) The length of the vagina relative to the length of the body is medium. (6) The length of the seminal receptacles relative to the length at the albumen gland is long. (7) The length of the glandular oviduct relative to the length of the body is long. (8) The posterior end of the distal penis is considerably to the left of the buccal mass (Fig. 38). (9) The distal end of the prostate touches the albumen gland but does not overlap the ventral surface of the albumen gland to any appreciable degree. (10) From external view there appears to be only one long but stubby finger-like seminal receptacle.

DISCUSSION. Specimens of orange-pink coloration were not differentiated electrophoretically from those with yellow-olive coloration. Pilsbry (1948 p. 808) noted three pale specimens without the typical black blotches on the body. These match the color pattern of *Succinea* cf. *pennsylvanica* and *S.* sp. B discussed below. However, we found no representatives of these taxa preserved in the alcohol collections at the ANSP.

Pilsbry's specimens of *S. o. chittenangoensis* were larger than those collected in 1983-1985. Pilsbry claimed that he found no specimens intermediate in shape between *S. ovalis* and *S. o. chittenangoensis* sympatric at Chittenango Falls. However, in ANSP lot #90132, collected by Pilsbry at Cazenovia, N.Y., in 1905, we observed one specimen intermediate in shell spire height. All others were *S. ovalis*.

This taxon is considered a discrete species on the basis of anatomy, and a sister species to *Novisuccinea ovalis* on the basis of anatomy and molecular genetics. There are ten anatomical differences between *N. chittenangoensis* and *N. ovalis* (see Table 7). *Novisuccinea ovalis* is globose with the penultimate whorl tightly coiled against the body whorl; the free oviduct originates from the ventral or right ventrolateral edge of the oviduct. The fertilization chamber, seminal receptacles and hermaphroditic duct are not pigmented or only very lightly pigmented; the posterior tip of the prostate overlaps the ventral anterior of the albumen gland; the distal penis and epiphallus are directly posterior to the buccal mass; the length of the vagina is long relative to the length of the albumen gland. The length of the glandular oviduct is short relative to the length of the body.

Novisuccinea sp. A (Minn. A; Minn. B) differs from *N. chittenangoensis* in that: (1) The posterior tip of the prostate overlaps the ventral anterior end of the albumen gland for at least one third the length of the latter. (2) The seminal receptacles are clearly separated as seen from external view. (3) The length of the vagina is long relative to the length of the body. (4) The length of the penis relative to the length of the body is medium or long. (5) As in *N. ovalis*, the distal penis ends directly posterior to the buccal mass or very close to this position. (6) As in *N. ovalis*, the length of the seminal receptacles divided by the length of the albumen gland is short.

Novisuccinea ovalis (Say 1817)

SHELL. Shell moderate in size, globose; short spire. Adult of 3 whorls. Suture deep, forming greatly-rounded whorls. Shell thin, yellowish-brown in color. Expanded body whorl. Lower lip of aperture rounded. Aperture at an angle to earlier whorls.

LIVING ANIMAL. First 1 to 1.5 whorls pale whitish or pink. Body whorl buff to olivaceous with grey or black blotches and streaks similar to *N. chittenangoensis*. Black transverse band separates first and last half of body whorl. Foot light yellow, orange at the edges, with grey stripes on the sides; dark patch on posterior dorsal portion of foot (as in *N. chittenangoensis*). Tentacles dark grey to black. Mantle edge flecked with orange. (Pilsbry, 1948, p. 804).

ANATOMY. Diagnostic features are as follows (see Figs. 41-43): (1) The body is rather globose (Fig. 41). (2) The penultimate whorl is tightly coiled and compressed against the body whorl. (3) There is considerable space between the posterior end of the albumen gland and the posterior end of the body whorl (Fig. 41). (4) Even in the most sexually mature specimens the glandular oviduct is short and compact (Fig. 41). (5) The distal penis and epiphallus are posterior to the buccal mass. 6) The free oviduct originates from the ventral or right ventrolateral aspect of the posterior end of the vagina. (7) The posterior prostate overlaps the ventral anterior end of the albumen gland (Fig. 43C). (8) The fertilization chamber, seminal receptacles and hermaphroditic duct are not pigmented or at most, lightly dusted with pigment. (9) Anterior to the fertilization chamber there is a swelling of the spermoviduct here called the anterior fertilization chamber. (10) The length of the seminal receptacles is short relative to the length of the albumen gland. (11) From external view there are two seminal receptacles.

DISCUSSION. Specimens of *S. ovalis* collected in Fairmont Park, Philadelphia in the early 20th Century were larger, with a relatively shorter spire, than specimen collected recently in New York State. But there is considerable variation in size and shape in the early specimens. See the discussion following the diagnosis for *N. chittenangoensis* for a detailed comparison of *N. ovalis* with *N. chittenangoensis*. Given the long vagina (relative to length of penis and/or length of body) and the manner in which the free oviduct encircles the spermathecal duct before becoming glandular, there is a constraint on the amount of space between the albumen gland and the free oviduct (Fig. 41). This short distance is evident in immature specimens, where the glandular oviduct is only a thin coiled tube, to fully mature specimens where the glandular oviduct has greatly swollen glandular lobes. This short distance is caused, in part, by the fact that the oviduct continues directly posterior as the massive spermathecal duct. The spermathecal duct then bends to the left where the free oviduct encircles it. The glandular oviduct is restricted, then, to a relatively shorter stretch of body whorl when compared with *N. chittenangoensis*, where the relative length of the vagina is medium (not long as in *N. ovalis*) and the free oviduct is the direct posterior continuation of the vagina as the spermathecal duct branches abruptly to the left off of the vagina.

The seminal receptacles of *N. ovalis* are very short and blunt, but not finger-like. There is more evidence of a separation into two seminal receptacles in *N. ovalis* than in *N. chittenangoensis*. In one pecimen of five, two were clearly discerned; in another two the tip of the receptacular mass was barely but discernibly lobed.

For a comparison with *N.* sp. A (Minn. A; Minn. B) refer to the discussion section for *N.* sp. A. below.

Novisuccinea sp. A (Minn. A; Minn. B)

SHELL. Minn. A: Shell small, moderate spire, slightly elongate; 3 whorls. Deep suture, rounded sides of whorls. Shell thick, pale tan in color. Body whorl moderately inflated. Minn. B: Shell moderate in size, short spire, not elongate; 3.25 whorls. Deep suture, rounded sides of whorls. Shell thick, light reddish brown in color. Body whorl inflated.

LIVING ANIMAL. Same in both Minn. A and B. First whorl peach-color; second whorl yellow-brown, sometimes dotted with black. Body whorl yellow-brown with black irregular dots above a black transverse band. Black band is almost disrupted at the center of the body whorl. One pale yellow dot above and one below black band. Yellow area anterior to black band followed by a thinner black band. Black lines below (anterior to) the second black band are parallel to the suture at first, then divide and follow veins. Diffuse dark band at lip of shell. A yellow line runs around penultimate whorl and first half of body whorl at suture. Many specimens are darker, with black dots on body whorl fused into streaks.

Edge of foot orange or peach fading to white at center of sole. No pigment around gonopore. Pale, opaque flecks of white or peach in mantle at shell edge. Black pigment on tentacles, dorsal head and neck, and in vertical stripes on foot. No black spot on posterior foot, as in *Novisuccinea ovalis* and *N. chittenangoensis*.

ANATOMY. Diagnostic features are as follows: (1) The body is elongated with the penultimate whorl and subsequent whorls turreted above the body whorl. (2) The albumen gland tip and most of the hermaphroditic duct projects into the penultimate whorl (contrast *N. ovalis* and some

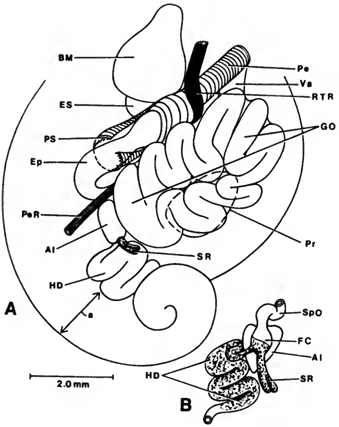


FIG. 44. *Succinea* cf. *pennsylvanica*. **A**, position of the reproductive organs in the body whorl. Prostate (Pr) is ventral to the glandular oviduct (dashed line). Epiphallus (Ep) has burst through the penis sheath (PS). There is considerable distance, a, between the hermaphroditic duct and the body whorl wall. **B**, albumen gland has been turned over 180 to show the fertilization chamber and the elongated seminal receptacles; they are lightly pigmented. Albumen gland is short.

specimens of *N. chittenangoensis*). (3) The glandular oviduct is long (contrast *N. ovalis*). (4) The end of the distal penis and epiphallus are posterior to the buccal mass or close to this position (contrast *N. chittenangoensis*). (5) The free oviduct is a posterior continuation of the vagina. (6) The posterior prostate overlaps the ventral anterior end of the albumen gland. (7) The fertilization chamber, seminal receptacles and hermaphroditic duct are heavily pigmented. (8) In three of the four individuals dissected there was an anterior fertilization chamber. (9) There are clearly two seminal receptacles seen from external view.

The two populations have some slight differences: (1) In Minn. A, the posterior section of the vas deferens is densely pigmented (not pigmented in Minn. B), and (2) the posterior vas deferens is tightly bound to the spermathecal duct by connective tissue (not so bound in Minn. B). (3) The length of vagina relative to the length of the penis in Minn. A is medium; in Minn. B it is long. (4) The relative length of the albumen gland is medium in Minn. A; long in Minn. B. (5) The length of the penis in Minn. A is long; medium in Minn. B.

DISCUSSION. These two populations differ from *N. ovalis* in that: (1) the body is elongate. (2) The penultimate whorl and subsequent apical whorls are turreted, not coiled closely pressed against the body whorl. (3) The albumen gland tip projects into the penultimate whorl (in fully mature individuals). (4) The two seminal receptacles are discernable clearly along their lengths from external view. (5) The free oviduct is a direct continuation of the vagina. (6) The fertilization chamber and associated organs are heavily pigmented. (7) The length of the glandular oviduct is long. (8) The length of the penis is medium or long.

The Minnesota populations differ from *N. chittenangoensis* in that: (1) the posterior prostate overlaps the ventral anterior end of the albumen gland. (2) The seminal receptacles are clearly separate as seen from external view. (3) The distal penis and posterior end of the epiphallus are directly posterior to the buccal mass. (4) The length of the vagina is long relative to the length of the body. (5) The seminal receptacles are short relative to the length of the albumen gland. (6) The length of the penis relative to the length of the body is medium to long.

SUCCINEA

Succinea cf. pennsylvanica Pilsbry 1948

SHELL. *Succinea pennsylvanica* paratypes; shell moderate in size, elongate; spire height

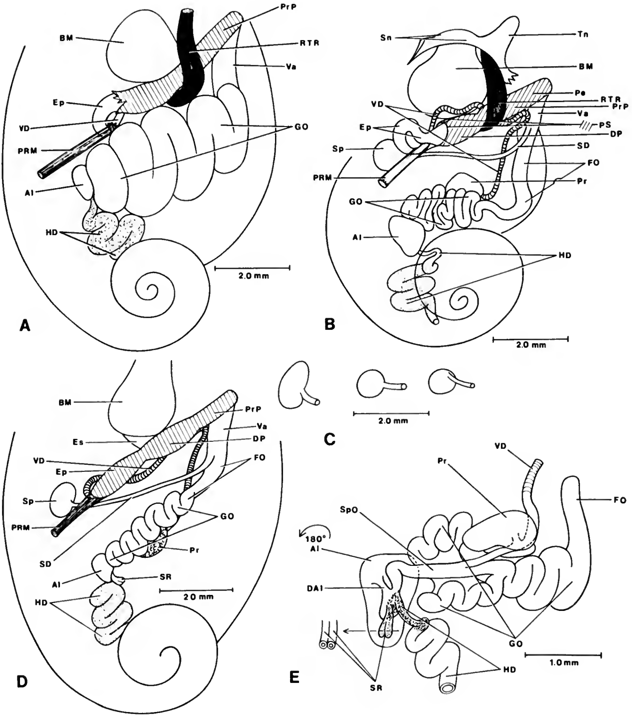


FIG. 45. *Succinea* cf. *pennsylvanica*. **A,** Fully mature individual, possibly a post-mating, egg producing individual. Epiphallus has burst through the penis sheath. Penis retractor muscle is attached to the vas deferens. **B,** sexually immature individual. Alternatively, this may be, as Emberton has suggested (personal communication), a mature individual that has laid its eggs thus depleting the glandular oviduct. Penis sheath is entire and encloses most of the distal penis. Penis retractor muscle attaches to the vas deferens and to the sheath. Slender spermathecal duct (SD) arises from mid-dorsal vagina (Va). **C,** variation in size and shape of the spermatheca as well as in position of attachment of the spermathecal duct. **D,** in this sexually immature individual the penis sheath encases the entire penis complex. The spermathecal duct arises from the left side of the vagina. Prostate (Pr) is far removed from the albumen gland. **E,** sexually mature individual with albumen gland turned over. Prostate is far removed from the albumen gland

variable, moderate to tall. Adults 3 1/4 whorls. Shell suture intermediate in depth (greater than *S. putris* and *S.* sp. (Wissahickon), less than *N. chittenangoensis*. Whorls slightly rounded. Shell of moderate thickness, light orange-brown ("ochraceous buff," Pilsbry 1948, p. 809) in color. Body whorl moderately expanded.

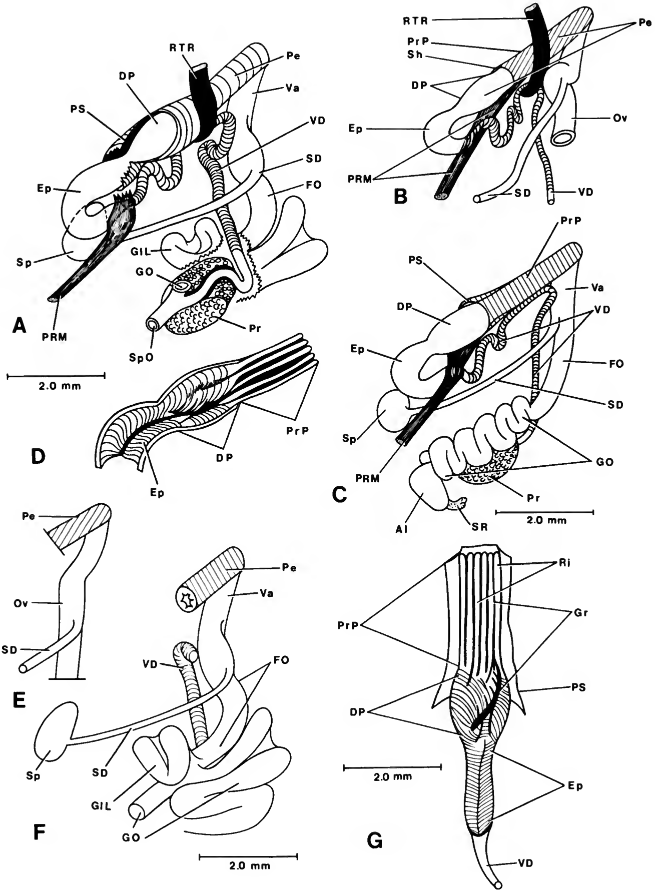
LIVING ANIMAL. "Soft parts creamy white spotted with brown or black," Pilsbry, 1948, p. 809.

ANATOMY. Diagnostic features are in Figs. 44-46: (1) The amount of the penis complex covered by the penis sheath is variable. In one immature specimen the sheath covered the entire penis complex (Fig. 45D). In fully sexually mature specimens three states were found: (a) The sheath appeared burst by the epiphallus with the penial retractor muscle attached to the vas deferens and a small splintered piece of sheath at the vas deferens (Fig. 45A, 46A); (b) The sheath covered the proximal and most of the distal penis without appearance that the epiphallus had burst through the sheath (Fig. 45B); (c) The sheath covered only the proximal penis (only one individual). The condition in "c" is essentially that seen in N. ovalis (Fig. 46B). The most commonly-encountered conditions appear to be a and b. (2) The penial retractor muscle of some individuals attaches to the penis sheath at the anterior or posterior end of the distal penis and again, after a short distance, to the loop of the vas deferens posterior to the penis (45B; 46B,C). (3) The body is globose with the penultimate whorl coiled and pressed to the body whorl (Fig. 44). (4) The penis has a very pronounced epiphallus seen from external view (Fig. 46B, D; 46A, B, C). In all cases there is a very strong constriction between the epiphallus and the distal penis. (5) The distal penis has an internal fleshy pad (Fig. 46 D, G). (6) The distal penis has an increased diameter compared with the proximal penis. (7) The vas deferens had pronounced circular muscles throughout. (8) The fertilization chamber and seminal receptacles are lightly pigmented (Figs. 45E, 44B, 46C). (9) The angle of the glandular oviduct to the mid-line of the body is greater than 45 degrees (Fig. 45A). (10) The length of the vagina divided by the length of the penis is medium. (11) The length of the vagina divided by the length of the body is medium. (12) The length of the albumen gland divided by the length of the body is short. (13) The proximal penis does not have a pronounced dilation near the genital opening (Fig. 45A-C). (14) There is no ampulla of the vas deferens at the prostate.

DISCUSSION. This species differs from the other species of *Succinea* discussed here by not having a penis sheath of mature individuals encasing the entire penis complex but most commonly enclosing the proximal and part of the distal penis. *S.* cf. *putris* is the only other species seen where the epiphallus of some individuals bursts through the sheath. Thus far this is the only species of *Succinea* we have studied with the rather globose body, thus the albumen gland is removed some distance (a, Fig. 44A) from the body wall. Only this species of *Succinea* has a pronounced and U-shaped epiphallus and a fleshy internal pad in the distal penis. The length of the vagina is medium, not short as in the other species of *Succinea* (in relationship to body length). The albumen gland is very small in contrast to that of the other species.

The spermathecal duct arises from the left side of the vagina in two individuals (Fig. 45D), from mid-dorsal vagina in one individual (Fig. 45B), and the right side of the vagina in one individual (Fig. 46B). In the last-mentioned case the vagina made a sharp twist to the right at mid-vagina, 60% of the way from the anterior end to the point where the spermathecal duct arose.

Pilsbry (1948 p. 809) described *N. pennsylvanica* with the type locality at Derrick City, McKean Co., PA. The shells of our study are not distinguishable from those in the type series (ANSP 142496). Pilsbry (1948) illustrated the gross reproductive system of *N. pennsylvanica* (p. 800, Fig. 429 E); he placed the species in *Novisuccinea* because he defined *Novisuccinea* as a group of species where the epiphallus projected as a free loop free from the penis sheath; the vagina was of moderate length; the free oviduct was typically very long. Pilsbry stated of this


RTR
Pe
DP
Va
PS
VD
SD
Ep
FO
GIL
Sp
GO
Pr
A
PRM
SpO
2.0 mm
RTR
PrP
Sh
Pe
DP
Ov
Ep
PRM
B
SD
VD
PrP
PS
Va
DP
VD
Ep
FO
SD
Sp
GO
PRM
Pr
C
AI
SR
2.0 mm
PrP
D
DP
Ep
Pe
Ov
SD
E
Pe
Va
VD
FO
Sp
SD
GIL
GO
F
2.0 mm
Ri
PrP
Gr
PS
DP
2.0 mm
Ep
G
VD

species that it differed from *N. ovalis* "by having the penial retractor and junction of [the] epiphallus and vas deferens entirely free from the penial sheath." He stated that in *S. pennsylvanica* "the long epiphallus forms a loop before receiving the retractor muscle. . ." He also stated that the vas deferens and penial retractor had no connection with the penis proper or its sheath (as in Figs. 8A, 9A, 10A).

Pilsbry's data for his *S. pennsylvanica* are scanty. The population we studied appears very similar to *S. pennsylvanica* as described by Pilsbry except for the penial retractor muscle connection to the sheath in some individuals. Accordingly we call this population *N.* cf. *pennsylvanica.*

Succinea putris Species Group

Succinea cf. putris (L.)

SHELL. Shell large, elongate, tall spire. Adults 3.5 whorls (maximum). Suture shallow, flat-sided whorls. Shell very thin, color unknown. Body whorl not expanded.

LIVING ANIMAL. No data

ANATOMY. Diagnostic features are (see Fig. 47): (1) The entire penis complex is covered by the penis sheath (Fig. 47A). In some individuals the epiphallus bursts through part of the sheath (Fig. 47B). (2) The penial retractor muscle connects to the posterior end of the sheath (Fig. 47A, B). (3) The body is elongate. (4) The distal penis does not have an internal fleshy pad (Fig. 46G). (5) As in *S.* cf. *pennsylvanica*, the vas deferens is circular with circular muscles throughout. (6) The fertilization chamber, seminal receptacles, and hermaphroditic duct are heavily pigmented, but not as black as seen in *N. chittenangoensis* (Fig. 47I). (7) The angle of the glandular oviduct to the mid-line of the body is 0 to 30° (Fig. 47A). 8) The relative length of the vagina is short (relative to penis length, body length, and spermathecal duct length). (9) The albumen gland is long relative to the glandular oviduct length; it is of medium length relative to the length of the body. The posterior end of the albumen gland projects up into the penultimate whorl in most individuals. (10) The proximal penis is markedly dilated near the opening (Fig. 47D-F). (11) There is an ampulla of the vas deferens at the prostate of most individuals (not seen in Fig. 47). (12) The spermathecal duct of some individuals is massive at the vagina then quickly tapers to a narrow tube (Fig. 47B). In other individuals it is narrow throughout (Fig. 47D-F). (13) The epiphallus of most individuals passes into the penis with no perceptible difference when seen in external view (Fig. 47A). In these cases the sheath encloses the entire penial complex. In other cases, especially when the epiphallus has burst through the sheath, there is a noticeable constriction at the posterior end of the distal penis at the juncture with the epiphallus. (14) There is no pronounced periceptacular sac. In one individual there was a slight posterior bulge of the fertilization chamber (x, Fig. 47G).

DISCUSSION. The anatomy of *Succinea putris* has been published by at least three investigators (Quick 1933; Rigby 1965; Patterson 1971). Their work is compared with ours in Tables 10 and 11. The comparison involves 15 characters. As previous workers did not state the number of animals

FIG. 46. *Succinea* cf. *pennsylvanica*. **A,** in this individual the sheath dorsally encloses only half of the distal penis (DP) but at the epiphallus it once fused to cover a short stretch of the epiphallus, but as seen the epiphallus burst through the part. The penial retractor muscle attaches to the vas deferens. Spermathecal duct arises from the right side of the vagina. **B,** penis sheath encases only the proximal penis; penis sheath attaches to the vas deferens and the penis sheath. **C,** another snail; penis sheath encases the proximal penis and only a small section of the distal penis. **D,G,** penis sliced open to show the nature of the folds in the three sections of the penis complex. Note in A-C how distinctly the epiphallus is set off from the distal penis by the marked narrowing of the connection. Note the fleshy pad of tissue in the distal penis (D, G). **E, F,** variation in the bending of the vagina when the spermathecal duct arises from the right side of the vagina (also see B)

Table 10. Comparison of populations considered to be *Succinea putris* by various researchers.

	Characters	Quick [1933] England (mostly)	Rigby [1965] Berkshire England	Patterson [1971] France	This paper Netherlands
1	Hermaphooditic duct strongly pigmented	yes	yes	?	yes
2	Seminal vesicles pigmented	moderately	?	moderately	strongly
3	Seminal vesicles (2) long and narrow	yes	yes	yes	yes
4	Perireceptacular sac present	no	as in Patterson pronounced	yes, dagger-shaped	no
5	a) epiphallus passes into penis imperceptably	yes	yes	no [1]	yes
	b) some individuals epiphallus has distinct shoulder or clearly discerned from penis	yes	no	yes [1]	yes
6	a) epiphallus entirely enclosed in penial sheath (individuals)	yes	yes	no	yes
	b) epiphallus of some individuals burst through penial sheath	yes	no	yes, of all [2] individuals	yes
7	The diameter of the vas deferens is wider than that of the spermathecal duct	yes	yes	yes	yes
8	The vas deferens is dilated at the prostate (has ampulla)	?	yes	?	yes
9	Duct of spermatheca dilated at vagina	no	no	no	± [3]
10	Vagina is long	yes	no	moderately	no [4]
11	Vagina slightly wavey	yes	yes	no	yes
12	Length of penis relative to length of vagina	1.65	>6.0	2	>6.0
13	Posterior prostate far removed from albumen gland	yes	yes	no	yes
14	Penis with discrete epiphallus	yes	no	yes	yes
15	Length of spermathecal duct/length of penis	0.76	1.8	1.07	0.75

---

[1] Patterson 1971). The penis constricts abruptly at juncture with the epiphallus.
[2] Patterson (1971). The penial sheath encloses only part of the epiphallus.
[3] This paper. The spermathecal duct of some indadition seen in Novisuccinea.
[4] This paper. The position on the vagina where t crosses the vason. In no case observed.

Table 11. Differences among anatomical data sets for the *Succinea putris* complex. Refer to Table 10. The distance coefficient is the number of differences divided by the number of characters compared. If there is a "?", the character could not be compared; thus the number of comparisons varied from 10 to 14. A ± was counted 1/2.

	Quick	Rigby	Patterson	This paper
Quick	-	0.54	0.67	0.25
Rigby		-	0.67	0.42
Paterson			-	0.73
This paper				-

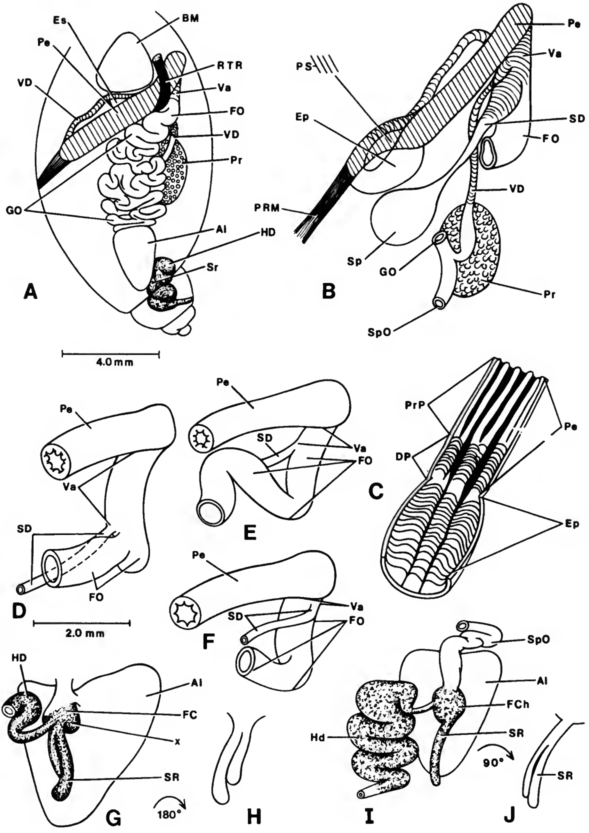
dissected and did not routinely consider variation of character-states, we cannot know how much apparent difference among populations is actually due to individual variation within a population. Some data could not be gleaned from previous publications. The most complete comparison is between our data set and Quick's. However, considering all data available, it does seen plausible that at least two species are involved, if not three. There appears to be a *Succinea putris* complex.

In dissecting open the penis, the proximal penis of our population was longer than the distal part. The latter was distinguished by a narrower irregular lumen, and by the coalescence of the long ridges of the proximal penis. The coalesced ridges were so contracted that they were strongly crenulated or noded. The cavity of the proximal penis was capacious. The epiphallus of all species is recognized by the internal structure of numerous circular folds (Fig. 47C). The seminal receptacles, from external appearance, appear to join before entering the fertilization chamber (Fig. 47 H, J).

Our *Succinea* cf. *putris* is most closely related to *Succinea* sp. B from Chittenango Falls and sp. C from Wissahickon Creek (Table 9; Figs. 54, 55). It differs from them in: (1) The vas deferens has circular muscles throughout. (2) The fertilization chamber and related organs are densely pigmented. (3) Some individuals have a massively wide spermathecal duct where it joins the vagina. (4) The length of the albumen gland relative to the length of the body is medium. (5) The length of the vagina relative to the length at the spermathecal duct is short. (6) When the penial complex of *S.* cf. *putris* is covered by a sheath, one cannot discern the transition from epiphallus to distal penis; this transition can be discerned in most individuals where the epiphallus bursts through the sheath. The epiphallus has not yet been seen to burst through the sheath in species B and C of the *S. putris* species complex.

The population of *Succinea* sp. B from Chittenango Falls differs from *S.* cf. *putris* by the additional following characters: It has a large pronounced perireceptacular sac (Fig. 51). The epiphallus is consistently distinct, set off from the penis by a constriction at the posterior end of the penis. The epiphallus is more slender than the distal penis. The epiphallus is always contained within the penis sheath. The vas deferens is weakly muscular throughout with longitudinal muscles. The length of the albumen gland relative to the length of the body is long.

The population of *Succinea* sp. C from Wissahickon Creek differs from *Succinea* cf. *putris* by the following additional characters: The vas deferens from the epiphallus to beneath the free oviduct is circular and with strong circular muscles; beyond that area to the prostate it is less muscled and ellipitical (i.e. flattened). The angle of the glandular oviduct to the mid-line of the body is between 35° to 40°. The length of the vagina relative to the length of the penis is medium.


Es
BM
Pe
RTR
VD
Va
FO
VD
Pr
GO
Al
HD
Sr
A
4.0 mm
PS
Pe
Va
Ep
SD
FO
VD
PRM
Sp
GO
Pr
B
SpO
Pe
Pe
SD
Va
FO
Va
SD
FO
D
2.0 mm
E
PrP
Pe
DP
C
Ep
Pe
Va
SD
FO
F
HD
Al
FC
x
SR
G
180°
H
SpO
Al
FCh
Hd
SR
90°
SR
I
J

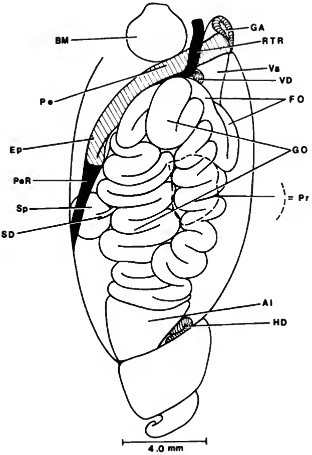


Fig. 48. *Succinea* sp. B. Relationship of organs to the body and penultimate whorls. Prostate (Pr) is far removed from albumen gland. It is difficult to distinguish three sections of the penial complex. Posterior end of albumen gland projects into penultimate whorl.

Succinea sp. B: Chittenango Falls, NY

SHELL. Shell large, elongate with tall spire. Adults 3.5 whorls. Suture shallow; flattened sides of whorls. Shell thin; pale yellow-gray in color. Body whorl moderately expanded.

LIVING ANIMAL. First 2 whorls grey, with narrow yellow band at the suture extending along the penultimate whorl as far onto the body whorl as the kidney. Large cream-white round dot just posterior to pericardium and kidney. A second smaller, irregular cream-white dot at base of kidney. Kidney seen through the shell as a sigmoidally-shaped intense yellow band running from the suture nearly to the edge of the shell, about 2/3 of the way up the body whorl from the aperture. Anterior to the kidney, animal golden-yellow, with golden mantle veins. At the mantle edge, faint irregular grey bands run perpendicular to the edge of the shell. These are very much fainter than in *N. ovalis* or *N. chittenangoensis.*

Foot of the snail pale yellow. Faint interrupted, grey, vertical lines anteriorly on the sides of the foot; grey speckles on the face between the tentacles; grey pigment inside the upper tentacles. Lower tentacles pale yellow except for the dark eyes at tips. Sole and posterior 1/3 of foot pale yellow. Grey pigment around the gonopore. No dark spot on dorsal posterior foot. Juveniles tend to be darker than adults; darkness of grey areas varies but is never as dark black as in *N. ovalis* or *N. chittenangoensis.*

ANATOMY. Diagnostic features are (see Figs. 48-51): (1) As in *S.* cf. *putris,* the entire penial complex is covered by a sheath. The epiphallus does not burst through the sheath (Fig. 48, 49, 50A, 51B,C). (2) The penial retractor muscle only connects to the posterior end of the sheath (Fig. 48) in most individuals; in some it also attaches to a loop of the vas deferens (Fig. 51C). (3) As in *S.* cf. *putris* the body is elongate. (4) The internal distal penis does not have a fleshy pad (Fig. 51D). (5) The vas deferens is unique among species studied here in that it is weakly muscled; the muscles are not circular but longitudinal (Fig. 50, 51B,C). (6) The fertilization

FIG. 47. *Succinea* cf. *putris.* **A,** relationships of organs to the body and penultimate whorls. About half the prostate is clearly seen lateral to the glandular oviduct. **B,** organs positioned as in A but with glandular oviduct removed to show that in this individual the epiphallus has burst through the penis sheath. Note section of spermathecal duct at the vagina is a very wide tube. **C,** penis sliced open to show nature of the folds in three sections of the penis complex. **D-F,** variation in where the spermathecal duct joins the vagina and the variance in length of oviduct. **G-J,** ventral aspect of the albumen gland showing variation in fertilization chamber and seminal receptacles. In G, x is that part of the fertilization chamber overlapping the seminal receptacles a bit.

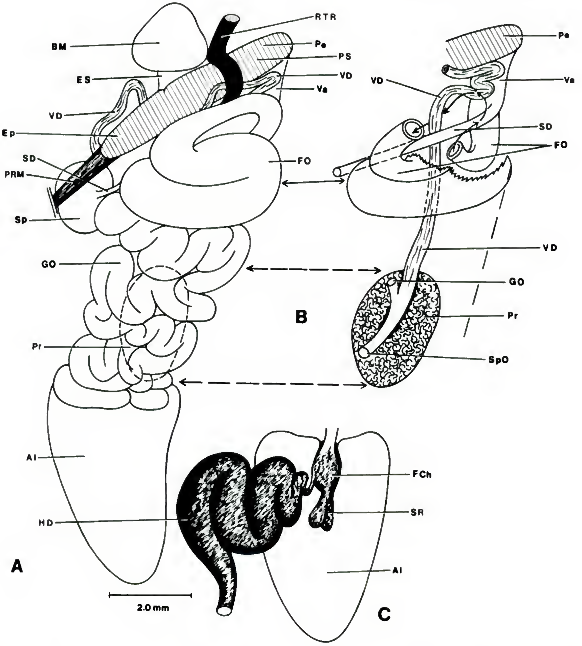


Fig. 49. *Succinea* sp. B. A, variation in pattern of coiling of glandular oviduct. Note very long albumen gland. **B**, glandular oviduct of A removed to show vas deferens and connections of the spermathecal duct to the vagina. Note long muscles of the vas deferens. **C**, albumen gland turned over 180 to show fertilization chamber and seminal receptacles

chamber and seminal receptacles are lightly pigmented (contrast *S.* cf. *putris*). (7) The angle of the glandular oviduct to the mid-line of the body is 0 to 30 . (8) The relative length of the vagina is short relative to body and penis length; long relative to spermathecal duct length (contrast *S.* cf. *putris*). (Figs. 49B, 50B, 51A). (9) The albumen gland is long (contrast *S. putris*). The posterior end of the albumen gland projects up intol the punultimate whorl. (10) the proximal penis is swollen at the opening (Fig. 48), but not to the extent seen in *S. putris*. (11) There is an ampulla of the vas deferens at the prostate of some individuals (AmV, Fig. 50), not others (Fig. 49B). (12) The spermathecal duct of all individuals is slender at the vagina (contrast S. putris)(Figs. 49B, 50, 51A). (13) The epiphallus of all individuals is distinguished from the

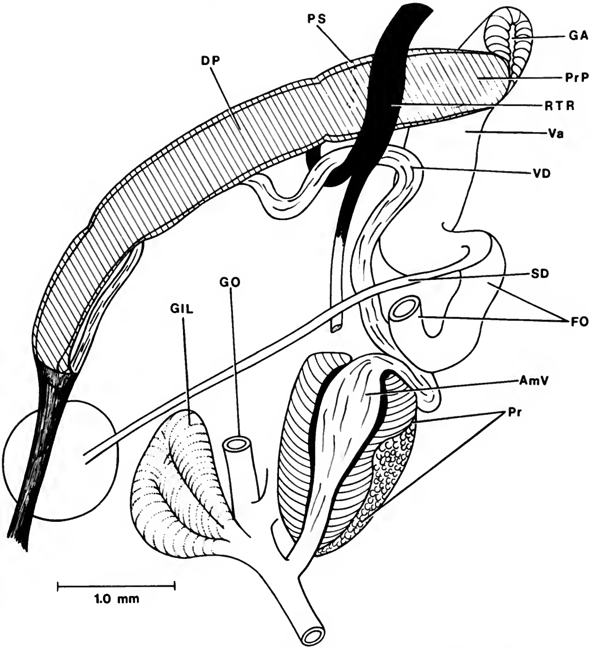
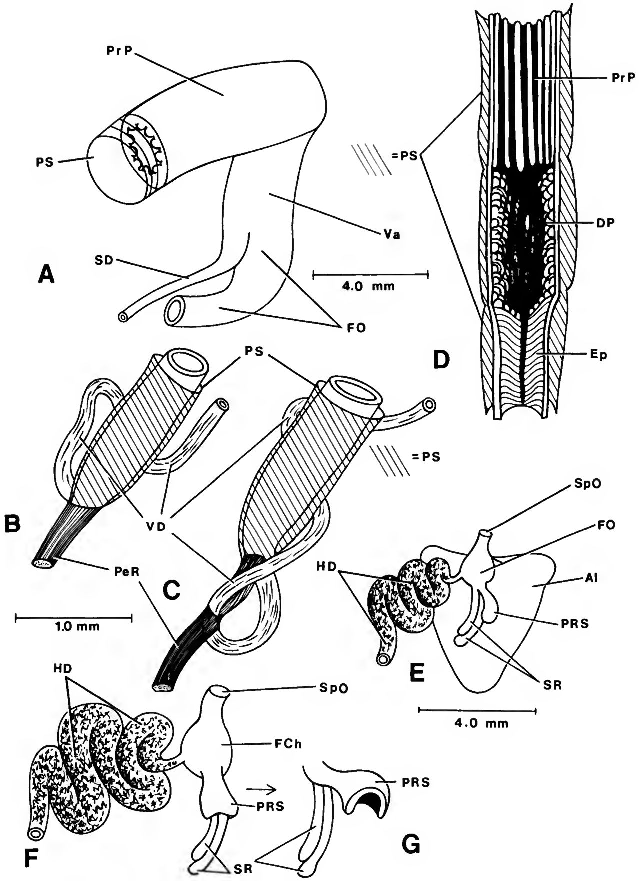


Fig. 50. *Succinea* sp. B. Glandular oviduct removed to show spermathecal duct, vagina, and vas deferens. Note ampulla (AmV) of vas deferens at the prostate. Spermathecal duct attaches to the vagina at right side; there is a pronounced bend of the vagina anterior to the junction.

distal penis due to a constriction at the junction. Differentiating these two parts of the penial complex may be difficult as the constriction may be subtle. No species of the *S.* cf. *putris* species complex seen thus far has the pronounced constriction seen in *S.* cf. *pennsylvanica* (Figs. 45, 46). (14) Only this species, of those studied here, has a pronounced perireceptacular sac (PRS, Fig. 51 F, G).

DISCUSSION. The spermathecal duct arose from the left side of the vagina in three of six individuals (Fig. 51), from the mid-dorsal surface in one; and from the right side in two (Figs. 49, 50). In only one of six individuals did the free oviduct (posterior to the spermathecal duct connection to the vagina) make a sharp twist to the right; in this case the spermathecal duct connected to the right side of the vagina. This situation has also been seen in *S.* cf.*pennsylvanica* (Fig. 46B).


PrP
PS
SD
A
Va
4.0 mm
FO
PrP
=PS
DP
D
Ep
PS
B
VD
=PS
PeR
C
1.0 mm
SpO
FO
HD
Al
PRS
E
SR
4.0 mm
HD
SpO
FCh
PRS
PRS
F
G
SR

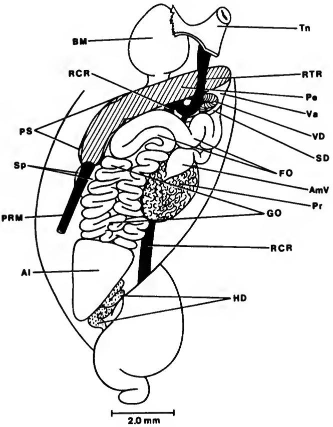


Fig. 52. *Succinea* sp. C. Relationships of organs to the body and penultimate whorls.

In some individuals of this population, the vas deferens makes a loop posterior to the penis before running anteriorly, and the penial retractor muscle fuses around the posterior bend of the loop. This is somewhat similar to the situation seen in *S.* cf. *pennsylvanica* (Fig. 46A).

This species is most similar to *S.* cf. *putris* and to *S.* sp. C than to any other we have studied. Differences with *S.* cf. *putris* have been discussed under that species (see pg. 39).

Succinea sp. C: Wissahickon Creek, PA

SHELL. Shell moderate to large, elongate, moderate to short spire (LAP:L >.70) Adults 3.25 whorls. Shell suture intermediate depth; rounded sides of whorls. Shell thin, golden-brown in color. Body whorl moderately expanded. (L:W=1.8).

LIVING ANIMAL. Shell apex (first 2 whorls) brownish-grey to chocolate. Body whorl yellow to orange with opaque gold band over kidney preceded by a bluish-grey band that sometimes bifurcates into 2 bands. Two cream-colored spots between the grey and gold bands; may be fused into one irregular splotch. Last half of body whorl has dense gold veins over yellow-brown to gold background. Faint grey circular band just above mantle edge. Sometimes a black patch on the penultimate whorl where the dorsal foot of the crawling animal touches the shell.

Foot and head pale cream, greyish on sides of foot. Grey lines on tentacles and neck. Grey patch on "forehead." Light grey pigment in the area of peristome. Gonopore area unpigmented. Dusting of black specks on posterior foot.

ANATOMY. Diagnostic features are (see Figs. 52-53): (1) The entire penial complex is covered by a sheath; the epiphallus does not burst through the sheath (Fig. 52, 53A). (2) The penial retractor muscle connects only to the posterior end of the penis sheath. (3) The body is elongate. (4) The internal distal penis does not have fleshy pad. (5) The vas deferens is circular with circular muscles from epiphallus to mid-vas deferens, thereafter it is a non-muscular flattened ellipse. (6) The fertilization chamber and seminal receptacles are not pigmented; the hermaphroditic duct is lightly pigmented. (7) The angle at the glandular oviduct to the mid-line of the body is 35 to 40 degrees. (8) The length of the vagina is medium relative to the length of penis, short relative to the body length and long relative to spermathecal duct length. (9) Albumen gland long; it does not project up into the penultimate whorl. (10) The proximal penis is not dilated at

---

Fig. 51. *Succinea* sp. B. A-D, variation in penis and vaginal complex characters. In A, spermathecal duct attaches to left side of vagina. In band C there is variation in the vas deferens relative to forming a loop and having the penial retractor muscle attaching to the loop. E-G, variation in the fertilization chamber, seminal receptacles, and perireceptacular sac.

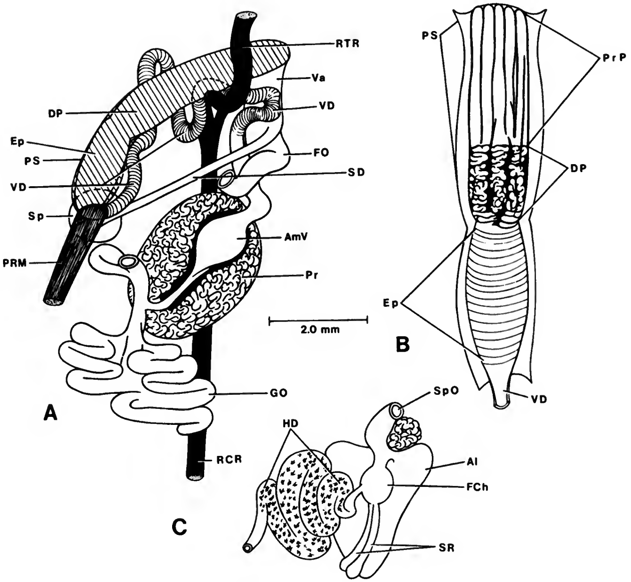


Fig. 53. *Succinea* sp. C. **A**, the glandular oviduct mostly removed to show connections of organs and ducts. Note pronounced ampulla of the vas deferens at the prostate AmV. **B**, penis sliced open to show folds characteristic of each section. **C**, ventral aspect the albumen gland showing fertilization chamber and elongate seminal receptacles.

the opening. (11) There is an ampulla of the vas deferens (AmV, Fig. 53A). (12) The spermathecal duct is slender at the vagina (all individuals). (13) The epiphallus of all individuals is distinguished from the distal penis due to a constriction at the junction. This species does not have the pronounced constriction seen in *S.* cf. *pennsylvanica* (Fig. 45E). (14) There is no perireceptacular sac.

DISCUSSION. The dorsal posterior aspect of the fertilization chamber of some individuals is saclike and slightly overlaps the seminal receptacles; this overlap does not constitute a perireceptacular sac as seen in Fig. 52 F, G for *Succinea* sp. B. The seminal receptacles do not appear to join before entering the fertilization chamber.

The spermathecal duct enters the vagina on its right side (Fig. 52, 53A). The vagina makes a twist posterior to this junction.

This species differs from *Succinea* sp. B in that: (1) The vas deferens does not make a loop posterior to the epiphallus as in *S.* sp. B and thus the penial retractor muscle does not attach to a loop of the vas deferens. (2) This species does not

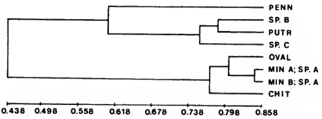


Fig. 54. Phenogram based on morphological data and similarity coefficient in Table 10.

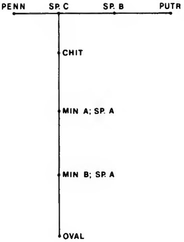


Fig. 56. Minimum spanning tree based on similarity coefficients in Table 10.

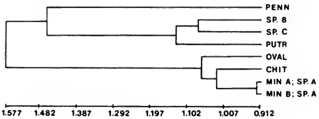


Fig. 55. Phenogram based on morphological data and distance coefficients in Table 11.

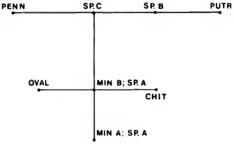


Fig. 57. Minimum spanning tree based on distance coefficients in Table 11.

have weak longitudinal muscles along the vas deferens as seen in S. sp B. (3) The fertilization chamber and seminal receptacles are not pigmented in this species. (4) the angle of the glandular oviduct to the mid-line of the body is greater in this species. (5) The length of the vagina relative to the length of the penis is greater in this species. (6) There is no perireceptacular sac in this species. (7) The penis of this species does not have a pronounced dilation at the opening.

PHENETIC RELATIONSHIPS

Similarity and distance coefficients are given in Tables 12 and 13. Corresponding phenograms are given in Figs. 54, 55; corresponding minimum spanning trees are given in Figs. 56, 57. The cophenetic correlations between phenograms and matrices are 0.919 for the distance analysis and 0.952 for the similarity analysis. The two minimum spanning trees are more in congruence with the phenogram based on distance coefficients. The most similar species within the *S.* cf. *putris* complex are *S.* sp. C and *S.* sp. B (78%) and *S.* sp. B and *S.* cf. *putris* (78%). *S.* sp. C is 73% similar to *S.* cf. *putris.*

In *Novisuccinea* the greatest similarity is between the two populations of Sp. A from Minnesota (84%). *N. ovalis* is 82% similar to population B of *N.* sp. A, and 78% similar to population A of *N.* sp. A. *Novisuccinea ovalis* is only 75%

Table 12. Matrix of morphological similarity coefficients. See Tables 8 and 9 for data.

	S. cf. penn.	*S. sp. B*	*S. putris*	*S. sp. C*	*N. ovalis*	*N. chit.*	*N. sp. A* Minn A	*N. sp. A* Minn B
S. cf. penn.	1.000							
S. sp. B	0.608	1.000						
S. putr.	0.588	0.784	1.000					
S. sp. C	0.627	0.784	0.725	1.000				
N. oval.	0.353	0.353	0.373	0.451	1.000			
N. chit.	0.490	0.451	0.510	0.549	0.745	1.000		
N. sp. A Minn A	0.373	0.373	0.431	0.471	0.784	0.804	1.000	
N. sp. A Minn B	0.412	0.490	0.471	0.549	0.824	0.765	0.843	1.000

Table 13. Matrix of morphological distance coefficients. See Tables 8 and 9 for data.

	S. cf. penn.	*S. sp. B*	*S. putr.*	*S. sp. C*	*N. oval.*	*N. chit.*	*N. sp. A* Minn A	*N. sp. A* Minn B
S. cf. penn.	0.000							
S. sp. B	1.474	0.000						
S. putr.	1.496	1.097	0.000					
S. sp. C	1.422	1.078	1.171	0.000				
N. oval.	1.765	1.688	1.667	1.524	0.000			
N. chit.	1.576	1.535	1.465	1.369	1.125	0.000		
N. sp. A Minn A	1.758	1.667	1.603	1.516	1.135	1.050	0.000	
N. sp. A Minn B	1.646	1.455	1.480	1.331	0.934	1.004	0.920	0.000

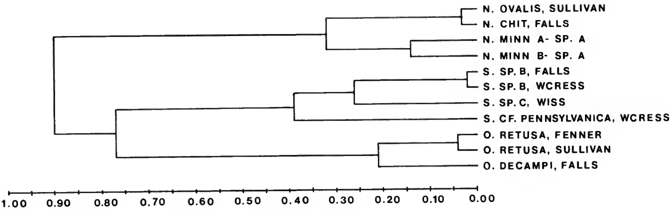


Fig. 58. Phenogram based on chord genetic distances for 11 populations and 23 loci.

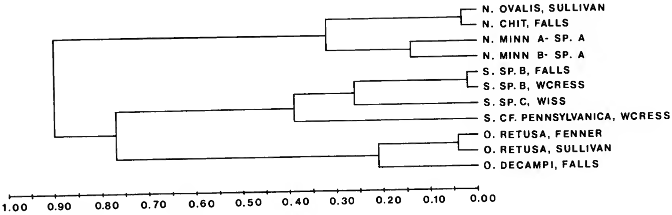


Fig. 59. Phenogram based on Rogers genetic distances for 11 populations and 23 loci.

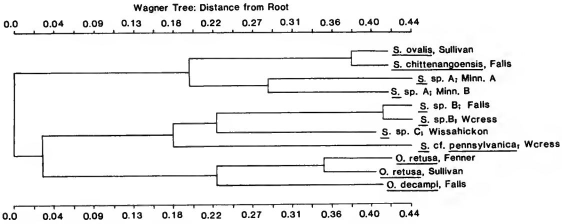


Fig. 60. Phylogenetic tree for 11 populations (using 23 loci) of Succineidae constructed using a distance-Wagner algorithm with optimization on Cavalli-Sforza and Edwards's chord distance. The tree is arbitrarily rooted at the midpoint of the longest path.

Table 14. Matrix of genetic distance coefficients, 23 loci. Below diagonal: Nei genetic distance; above diagonal: Cavalli-Sforza & Edwards (1967) chord distance.

Population		*N. oval.* Sullivan	*N. chit.* Falls	*S. sp. B* Falls	*S. sp. B* W'cress	*S. cf. penn* W'cress	*O. ret.* Fenner	*O. ret.* Sullivan	*O. dec.*	*N.bsp.bA* Minn. A	*N. sp. A* Minn. B	*S. sp. C*
N. ovalis	Sullivan	-	0.080	0.860	0.857	0.882	0.824	0.808	0.830	0.502	0.434	0.830
N. chit.	Falls	0.004	-	0.860	0.857	0.879	0.826	0.809	0.831	0.483	0.427	0.829
S. sp. B	Falls	2.621	2.670	-	0.063	0.566	0.796	0.787	0.796	0.868	0.864	0.391
S. sp. B	W'cress	2.588	2.626	0.001	-	0.558	0.799	0.786	0.794	0.862	0.858	0.392
S. cf. penn.	W'cress	4.248	4.314	0.524	0.521	-	0.781	0.782	0.794	0.869	0.854	0.462
O. retusa	Fenner	1.975	1.973	1.594	1.628	1.439	-	0.131	0.395	0.885	0.860	0.769
O. retusa	Sullivan	1.857	1.852	1.565	1.585	1.539	0.018	-	0.357	0.859	0.838	0.756
O. decam.	Falls	2.070	2.072	1.589	1.608	1.586	0.225	0.187	-	0.848	0.843	0.745
N. sp. A	Minn A	0.402	0.370	2.815	2.712	2.933	4.081	2.957	2.256	-	0.293	0.846
N.sp. A	Minn B	0.284	0.269	3.036	2.905	2.671	2.760	2.325	2.223	0.104	-	0.838
S. sp. C	Wiss	2.431	2.464	0.227	0.234	0.325	1.333	1.288	1.211	2.519	2.414	-

Table 15. Matrix of Nei's genetic similarity and distance coefficients (31 loci). Below diagonal: Nei (1972) genetic distance; above diagonal: Nei (1972) genetic identity

Population		*N. ovalis*	*N. chitt.*	*S. sp. B*		*O. retusa*		*O. d. gouldi*
		Sullivan	Falls	Falls	Watercress	Fenner	Sullivan	Falls
N. ovalis	Sullivan	-	0.996	0.122	0.124	0.169	0.182	0.16
N. chitt.	Falls	0.004	-	0.120	0.122	0.170	0.183	0.16
S. sp. B	Falls	2.105	2.122	-	0.998	0.234	0.239	0.235
S. sp. B	Watercress	2.091	2.103	0.002	-	0.223	0.230	0.226
O. retusa	Fenner	1.780	1.773	1.453	1.500	-	0.987	0.753
O. retusa	Sullivan	1.705	1.697	1.433	1.470	0.013	-	0.775
O. d. gouldi	Falls	1.835	1.831	1.449	1.486	0.284	0.255	-

similar to *N. chittenangoensis.*

The two phenograms clearly show the considerable distinction between species groups relegated respectively to *Novisuccinea* and *Succinea* .

ELECTROPHORETIC RESULTS

Initial electrophoresis in 1983 of seven populations of New York snails (Table 1) yielded results for 31 loci, 30 of which had no overlap in gene frequencies between at least two species and therefore were diagnostic for assessment of taxonomic relationships. Thirteen loci were polymorphic in at least one sample. In 1984-1985, four additional populations were added to the data set: two from Minnesota, one from Philadelphia, and an additional taxon from Chittenango Falls, N.Y. (Table 2). Seven electrophoretic loci were not scorable for one or more of the new populations and one locus (EST 2) was identical for all populations, leaving a set of 23 loci that contained information for all 11 populations. The allele frequencies are given in Appendix I, Table 1. The overall genetic variabilty is given in Appendix I, Table 2. In the three years of field study, we did not find *N. ovalis* sympatric with *N. chittenangoensis.*

The results are summarized in matrices of genetic distance. In Table 14, Nei's D is below the diagonal and Cavalli-Sforza and Edwards's chord distance is above the diagonal for 11 populations and 23 loci. The phenogram based on the chord distances is given in Fig. 58. The cophenetic correlation is 0.995. Table 15 gives Nei's D and I values for the first seven New York populations and 31 loci. We use Nei's D because it has become a standard for comparison, although Cavalli-Sforza and Edwards's D represents the data more accurately. Table 16 gives Rogers (1972) distance below the diagonal and similarity above the diagonal. The phenogram based on Rogers distances is given in Fig. 59. The cophenetic correlation is 0.993. A comparison of Nei's D with 23 and 31 loci shows a decline in genetic distance when more loci are used. These additional loci were conservative for the taxa assessed.

The several indices of genetic distance gave essentially the same pattern of relationships

Table 16. Matrix of Rogers (1972) Genetic similarity (above diagonal) and distance coefficients (below diagonal).

	Population		*N. oval.*	*N. chit.*	*S. sp. B* Falls	*S. sp. B* W'cress	*S. cf. penn*	*O. ret.* Fenner	*O. ret.* Sullivan	*O. dec.*	*N. sp. A* Minn. A	*N. sp. A* Minn. B	*S. sp. C*
1	*N. ovalis*	Sullivan	-	0.969	0.093	0.099	0.052	0.152	0.171	0.139	0.638	0.714	0.123
2	*N. chit.*	Falls	0.031	-	0.089	0.095	0.053	0.154	0.175	0.140	0.661	0.725	0.126
3	*S. sp. B*	Falls	0.907	0.911	-	0.985	0.578	0.203	0.214	0.206	0.063	0.066	0.743
4	*S. sp. B*	W'cress	0.901	0.905	0.015	-	0.576	0.199	0.211	0.203	0.069	0.072	0.734
5	*S. cf. penn.*	W'cress	0.948	0.947	0.422	0.424	-	0.242	0.222	0.213	0.072	0.097	0.678
6	*O. retusa*	Fenner	0.848	0.846	0.797	0.801	0.758	-	0.960	0.780	0.021	0.080	0.276
7	*O. retusa*	Sullivan	0.829	0.825	0.786	0.789	0.778	0.040	-	0.798	0.053	0.111	0.289
8	*O. decampi*	Falls	0.861	0.860	0.794	0.797	0.787	0.220	0.202	-	0.110	0.125	0.301
9	*N. sp. A*	Minn A	0.362	0.339	0.937	0.931	0.928	0.979	0.947	0.890	-	0.857	0.098
10	*N. sp. A*	Minn B	0.286	0.275	0.934	0.928	0.903	0.920	0.889	0.875	0.143	-	0.119
11	*S. sp. C*	Wiss.	0.877	0.874	0.257	0.266	0.322	0.724	0.711	0.699	0.902	0.881	-

Table 17. Number of loci fixed for alternate alleles. Twenty-three loci were examined for all comparisons except (*) = 31 loci.

		N. oval.	*N. chit.*	*N.* sp. A Minn. A	*N.* sp. A Minn. B	*S. cf. penn.*	*S.* sp. B	*S.* sp. C	*O. ret.*	*O. dec.*
N. ovalis		-								
N. chit.		0*	-							
N. sp. A	Minn. A	4	3	-						
N. sp. A	Minn. B	2	2	1	-					
S. penn.		19	19	20	18	-				
S. sp. B		26*	26*	20	18	7	0*			
S. sp. C	Wiss.	16	15	18	17	4	1	-		
O. retusa		22	22*	18	18	14	19*	11	0*	
O. decampi		23*	23*	20	18	15	21*	13	4*	-

among the taxa. A distance-Wagner algorithm using the Cavalli-Sforza and Edwards's chord distance gave the highest cophenetic correlation, 0.998 after optimization. A tree was produced by rooting at the midpoint of the longest path because no information on ancestors was available (Fig. 60).

The allopatric populations of *Novisuccinea ovalis* and *N. chittenangoensis* are similar enough genetically to be populations of the same species. The Nei's D separating them is only 0.004, whereas the distance between two populations of *Oxyloma retusa* (Lea) from the same two localities is 0.018 (Table 14). *N. ovalis* and *N. o. chittenangoensis* share alleles at all loci examined, as do two populations each of *O. retusa* and the *Succinea* sp.B (Table 17). Species-level Nei's distances are on the order of 0.2 for *O. decampi gouldi* Pilsbry and *O. retusa*. The two Minnesota populations differ by Nei's D = 0.104 and are fixed for alternate alleles at only 1 locus, suggestive of populations or closely related species, although it is not possible to assign taxonomic level based on genetic distance alone.

The original specimens sent to us for electrophoresis from Chittenango Falls were labeled *Succinea ovalis*, *Succinea chittenangoensis*, and *Oxyloma* sp. (Table 3). It was clear from the electrophoretic results and inspection of shells that there were more than three species. Figure 60 and Table 15 show that 5 species could be identified from the Chittenango Falls area in 1984 (one more was found in 1985). Specimens originally labeled *Succinea chittenangoensis* were very distinct from both *N.ovalis* and true *N. chittenangoensis*, which we identified by comparing with Pilsbry's own specimens. The unknown taxon had a genetic distance of over 2.0 from the two *Novisuccinea* taxa; this was the greatest distance of all comparisons (Table 15). This unknown taxon, which we labeled *S.* sp. B, was distinct from the two *Novisuccinea* at 26 of 31 loci examined (Table 17).

The unknown specimens from Chittenango Falls were re-collected in 1985, and a second species appeared with a Nei's D = 0.52 from *S.* sp. B. This second species (= *S.* cf. *pennsylvanica*) was found only in 1985 and only in the watercress below the falls, whereas *S.* sp. B was found in all years and both on the falls and in the watercress beds. Nei's D = 0.001 separates the two populations of *S.* sp. B. Sympatric specimens of *S.* sp. B and *S.* cf. *pennsylvanica* were fixed for alternate alleles at 7 of 23 loci (Table 17), confirming their separate species status. The animals with similar shells from Wissahickon Creek, PA, were more allied genetically to the *S.* sp. B than to any other taxon (D=0.2); the two taxa were fixed for alternate alleles at only 1 locus (Table 17).

Overall, considering electrophoretic data, there are three species groups: one containing the *Oxyloma* spp., one containing *N. ovalis*, *N. chittenangoensis*, and the two Minnesota taxa, and a third containing the three Succinea species from Chittenango Falls and Wissahickon Creek. The third group is more closely related to *Oxyloma* than to *Novisuccinea* (Table 17, Fig. 60). The data clearly show that *Novisuccinea* is a valid genus.

DISCUSSION

Generic Concepts

On the bases of both morphological and molecular genetic data it is clear that three genera are involved. It was fortuitous that *Oxyloma* was used as an outgroup for the molecular genetic comparisons because *Oxyloma* has been long established as a distinct genus of Succineidae on the basis of comparative anatomy while all of the other species treated here were previously considered to belong to *Succinea*. *Oxyloma* Westerlund 1885 was defined by Pilsbry (1948) as a group of species with the penis terminating posteriorly in a small appendix. The penis and epiphallus are enclosed in a sheath; the epiphallus is sinuous or closely convoluted. *Succinea* Draparnaud (1801) was defined by Pilsbry (1948) as a group of species with the penis lacking an appendix and with the epiphallus either enclosed in the sheath or emerging from the sheath. The epiphallus is not sinuous or closely convoluted.

Pilsbry (1948) described *Novisuccinea* as a new section of *Succinea* to encompass the *Succinea ovalis* species group where "the end of the penis and adjoining part of the epiphallus project in a loop free from the penial sheath." On the basis of this anatomical study we have redefined *Novisuccinea* and elevated this taxon to full generic rank using a number of characters (see p. 28). Part of the distal penis and the epiphallus of *S. pennsylvanica* are free from the sheath in some individuals. This superficially resembles the condition seen in all individuals of species assigned to *Novisuccinea*. However, the distal penis with its posterior blind sac and the position and size of the initial portion of the epiphallus of species assigned to *Novisuccinea* are clearly discernable character states serving, in part, to define the genus. Another important character-state serving to define *Novisuccinea* is the 360 degree loop of the free oviduct around the spermathecal duct. Accordingly, it is clear to us that *S.* cf. *pennsylvanica* belongs to *Succinea* s.s.

An unexpected finding of the molecular genetic study was that *Succinea* is much more closely related to *Oxyloma* than it is to *Novisuccinea* (Figs. 58-60). This could not have been predicted on the basis of the anatomical data available. It is clear that the penial appendix and folded epiphallus of *Oxyloma* do not set *Oxyloma* apart in one clade with taxa lacking these character- states belonging in a *Succinea* clade. The 360 degree loop of the free oviduct around the spermathecal duct and the distal-penis and epiphallus character-states mentioned above are associated with the genetic separation of *Novisuccinea* from *Oxyloma* and *Succinea*.

Species Concepts

The literature on Succineidae and particularly *Novisuccinea chittenangoensis* has been clouded by misidentifications and failure to recognize the presence of more than one species. For example, both Thomée (1986) and Aloi (1986) confounded several of the Chittenango Falls species, although they gave valuable descriptions of the general habitat of these species. Their fecundity data are probably based on the species we are here calling *Succinea* sp. B. The *N. chittenangoensis* of Aloi and Ringler (1982) is really S. sp. B, while their *S. ovalis* is the real *N. chittenangoensis* and *O. virrilli* [sic] is equivalent to the two species called *O. retusa* and *O. decampi* gouldi by Pilsbry. Grimm (1981) gave descriptions of the shell shape, size, number of whorls, and body pigment of *S. chittenangoensis* that indicated he also had specimens of *S.* sp. B. The recovery plan published in the Endangered Species Technical Bulletin (Anon. 1984) contains a photograph of the same *S.* sp.B instead of *S. chittenangoensis.*

In this paper, we have not attempted to determine the correct names for the two species of *Oxyloma* at Chittenango Falls. It is possible that *Oxyloma decampi gouldi* (Pilsbry 1948) is equivalent to *O. verrilli* Bland, as suggested by Grimm (1981). Harris and Hubricht (1982) accepted *O. gouldi* (Pilsbry) as a valid species from New England, but claimed that *O. retusa* does not occur there; they synonymized *O. verrilli* under *O. groenlandica* Möller and said it was limited to Canada. Their scheme leaves only one name available for *Oxyloma* at Chittenango Falls, and therefore must be incorrect. To confuse matters further, Hubricht (1985) synonymized *O. decampi gouldi* Pilsbry under *O. retusa* (Lea), leaving no names available for Chittenango Falls specimens. We continue to use the names *O. retusa* and *O. d. gouldi* for species found at Chittenango Falls, consistent with Pilsbry's usage, although we expect that more detailed comparison with topotypical material will show one or both are species distinct from the topotypical populations.

Species concepts used here were based on: (1) gross qualitative anatomy, (2) relative organ and body sizes and shapes, (3) detailed qualitative and quantitative anatomy, (4) consideration of artifacts due to preservation, (5) consideration of artifacts due to the state of reproductive system maturity. Shell data corroborate species separation in some cases, but poorly discriminate some taxa, such as *Succinea* cf. *pennsylvanica* and *S.* sp. B. (Table 5).

Historically, land snail species concepts have been based on qualitative gross anatomy with the reproductive system either removed from the body or displayed artificially relative to the real and natural position within the body. The number of animals dissected has not been given nor has variation been documented. How organs connect or relate to each other positionally have not been clearly shown. We suspect that most previous work was based on only one or two dissections; some authors may have used three to five individuals. Only two papers that we know of have dealt with morphological variation: Solem (1981, Fig. 53) and Emberton (1985).

Emberton (1985), in an excellent paper, carefully documented seasonal changes in the reproductive system of the polygrid *Triodopsis*. He clearly showed that "the relative size or shape of any pulmonate reproductive organ should be used as a taxonomic character only with caution and with a full knowledge of its range of intraspecific variation." He also, however, acknowledged the reality that the reproductive system "provides a rich source of phylogenetically and taxonomically useful characters. . . ." This topic bears on the problem of artifacts due to state of maturity. We were careful to use animals of approximately the same advanced stage of sexual maturity and reproductive organ development, beyond stage 2 as defined below.

Three stages reproductive organ development were obvious throughout this study: (1) Initial development was evident where the glandular oviduct was a thin undulating tube with no glandular lobes. The prostate and albumen gland were correspondingly minute and clearly far from attaining full size. (2) The intermediate stage occurred when the glandular oviduct was a wide, undulating tube and the glandular lobes were clearly evident but not so fully loaded that the whole glandular oviduct filled the dorsal space between the penis and the posterior end of the body whorl. The prostate and albumen glands were nearly full sized relative to stage three. (3) The final stage was seen when the glandular oviduct was fully charged, i.e. swollen to fill the large dorsal volume of the body whorl from buccal mass or penis to the posterior wall of the body whorl. The prostate and albumen gland attained maximum size relative to the constraining length of body. In no case have we found a stage 3 development of the glandular oviduct and a stage 2 or less development (small size) of the albumen gland, prostate, or seminal receptacle.

Admittedly there is much we do not know (nor have other land snail systematists over the past 100 years concerned themselves with the problems). There are probably changes that take place after sperm exchange, egg production and egg laying that cause modifications in size and configuration of organs. These would presumably be post stage three changes. If animals are annuals, as has been speculated, they would presumabbly mature rapidly, reproduce and die off before the end of one full year. Accordingly the immature and mature reproductively active individuals would most likely be collected. It would be useful to learn if there is a seasonal post-reproductive period before death and, if so, how long and to what effect on the reproductive organs.

By studying the reproductive organs in precise relationship to body shape and size using discrete anatomical markers, it was possible to quantify positional relationships of organs, relative organ length, and constraints on certain organ sizes and deployment caused by developmental constraints. These procedures provided numerous character-states of value in distinguishing among species in addition to those usual gross anatomical characters historically used. This broadened data base has shown us that what has been called *Succinea ovalis* is actually a species complex and that the data previously used to define the species actually define the generic level. The data base has further been broadened by detailed qualitative anatomical data. For example, historically, no attention was paid to the musculature, shape, or discrete twists found in the vas deferens, or to the fact that the epiphallus was or was not markedly distinct from the distal penis, etc.

This expanded data base distinguishes *Novisuccinea ovalis* from *N. chittenangoensis*. The five specimens of *N. ovalis* that we dissected-come from three widely-separated populations, one being the topotypical locality. No significant difference was seen among specimens of these populations, so the data were pooled. In all cases the albumen gland is well separated from the posterior end of the body whorl (Fig. 41), the posterior end of the penis complex is close to the midline of the body, and the glandular oviduct is restricted to a short stretch between the spermathecal duct and the albumen gland. A constraint of development appears to be associated with the configuration of the glandular oviduct; the vagina is elongated and continued posteriorly to finally bend left as the wide spermathecal duct. The glandular oviduct of all species of *Novisuccinea* studied begins posterior to the 360 degree loop of the free oviduct around the spermathecal duct. The posterior position of the spermathecal duct in essence squeezes posteriorly the space for the glandular oviduct. In the most sexually mature specimens of *N. ovalis* seen, the glandular oviduct covers the spermathecal duct but does not extend more anteriorly than the spermathecal duct due to the constraint in the extent to which the glandular lobes can expand and the binding of the free oviduct as it coils around the spermathecal duct.

As seen in Table 9, there are 10 character-state differences between *N. ovalis* and *N. chittenangoensis*. In the latter, the length of the vagina is medium, not long both in relationship to body and penis length; the length of the glandular oviduct is long, not short. In *N. chittenangoensis* the spermathecal makes an abrupt right-angle turn to the left from the vagina with the free oviduct the posterior continuation of the vagina (Fig. 39A, contrast *N. ovalis*, Fig. 43A). The body of *N. chittenangoensis* is elongated as is the shell (contrast *N. ovalis*). The fertilization chamber, seminal receptacles and hermaphroditic duct are jet black with melanin pigment; those of *N. ovalis* are lightly pigmented or not pigmented. The mantle of *N. chittenangoensis* has a unique pigment pattern.

Solem (1976) pointed out that *N. ovalis* and *N. chittenangoensis* have been collected several times living sympatrically at Chittenango Falls, and that there is no intergradation of shell types between the two taxa. Given all of this evidence it is clear to us that two species are involved. We cannot agree with Solem (1976) that in genitalia *N. ovalis* and *N. chittenangoensis* show no differences except those regarded as seasonal (i.e. swollen hermaphroditic duct and enlarged prostate), or that differences in shell spire height (a character correlated with body shape and distribution of organs within that shape) "could result from a single mutation." He concluded by calling *N. chittenangoensis* a mutant form, the "result of a simple dominant genetic change." Solem (1976) used specimens from Illinois that were presumed to be *N. ovalis*. They may not necessarily be *N. ovalis*. We feel that Solem was correct in stating that the prostate and hermaphroditic duct of his specimens of *"N. ovalis"* indicated lack of stage 3 sexual activity. However, he does illustrate several major differences between his *"N. ovalis"* and *N. chittenangoensis:* (1) The seminal receptacles of the latter appear as a single finger-like projection while in the former they are clearly separated. (2) The pigmentation on the seminal receptacles and hermaphroditic duct in the former is jet-black while there is no pigmentation on the seminal receptacle and very little on the hermaphroditic duct of the former. These two character-states given above match our observations, but there are character-states illustrated for Solem's *"N. ovalis"* that, if they are correct, differ from our N. ovalis: (1) The seminal receptacles of his "N. ovalis" arise proximal to the albumen gland, not from the fertilization chamber imbedded in the albumen gland as in *N. chittenangoensis* and *N. ovalis* s.s. (2) The hermaphroditic duct is seen joining the distal end of one seminal receptacle in his *"N. ovalis."* In the taxa that we studied, the hermaphroditic gland always enters the fertilization chamber proximal to the fseminal receptacles. These differences coupled with shell differences are sufficient to indicate that Solem was dealing with two species, not different phenotypes of the same species and certainly not differing by a single mutation. It is probable that he was not looking at *N. ovalis* s.s. Contrary to his concluding statement, he did not examine typical *S. ovalis*. One cannot presume to know how much or what kinds of genetic differences regulate the morphological differences seen, but more than one gene is surely involved.

The Minnesota populations differ from *N. ovalis* in six character states (Tables 8, 9). The two Minnesota populations are 84% similar (morphological data) and are 78 and 82% similar to *N. ovalis*, respectively. *Novisuccinea ovalis* is 75% similar to *N. chittenangoensiss:* not including shell or mantle pigmentation patterns, there are 6 to 8 differences out of 39 characters (51 character-states as listed in Table 8). The average similarity among genera is 44±6% (Table 12). The least similar species among the species of *Succinea* we studied were 61±0.02% similar (*S.* cf. *pennsylvanica* vs. other species of *Succinea*). Species of the *S. putris* complex are 76±0.03% similar. When three different populations of *Novisuccinea ovalis* were studied there was 100% similarity among them. Given this lack of variation among populations of the same species, and considering the degree of difference among the populations as discussed above, it is reasonable to consider seven of the eight populations to be distinct species on the basis of internal morphology (Minn. A and B are not considered distinct species).

This contention is strengthened by the molecular genetic data. There are considerable genetic divergences between the three species of *Succinea* studied (Rogers' D≥0.25 among *S.* cf. *pennsylvanica*, *S.* sp. B and *S.* sp. C). Also, the relationships among these three species based on the genetic data are generally the same as those based on morphological data (compare Figs. 60

and 55). There is considerable genetic difference both between *Novisuccinea ovalis* and *N. chittenangoensis*, and the two populations of *Novisuccinea* from Minnesota (Rogers' D≥0.30). It is clear that there are discrete species-level differences between *N. ovalis* and *N. chittenangoensis* and the two Minnesota populations. However, the genetic data are of no help in distinguishing *N. ovalis* and *N. chittenangoensis* as distinct species.

Molecular Genetics, Morphology, and Taxonomic Rank

The strengths, weaknesses, and limitations of allozyme genetic data sets are clearly revealed in this study. One cannot equate a certain amount of genetic distance with taxonomic levels. However, generalities can often be made when a number of species have been studied and the system calibrated. To avoid circularity, in this study the initial species concepts were based on anatomical data. The baseline for determining how much difference was needed to discriminate among species was the population differences using topotypical and regional *N. ovalis.* There were no anatomical differences among these populations involving the characters listed in Table 8. Accordingly it is probable that populations ≥90% morphologically similar would belong to the same species. On this basis *N. ovalis* and *N. chittenangoensis* are distinct species; it is marginal whether or not the two populations of Minnesota *Novisuccinea* are different species. Now the molecular data can be added. Two populations of *Succinea* sp. B showing no morphological differences had a Rogers' genetic distance (D) of 0.015; the two populations of *Oxyloma retusa* had a D of 0.04. The generality gleaned from the literature is that in the overwhelming number of cases studied, populations of the same species have a D of ≤ 0.06. Likewise, D≥ 0.16 are usually associated with differences between species.

This genetic study is in agreement with the established view but with two special situations. *Novisuccinea ovalis* and *N. chittenangoensis* have a D value of 0.031, indicative of a population-level difference. However, it is well established that it is possible for distinct species to have D as low as this. In other words, there are situations in which allozyme data will not serve to discriminate species. A number of such cases have been reviewed (Davis et al. 1981). One concept currently much in vogue is that species that have recently diverged have not been separated long enough to accumulate sufficient genetic distance to be recognized as species on the basis of D. It may be true in this case, because *N. chittenangoensis* is localized at Chittenango Falls and is obviously closely related to *N. ovalis.* With the retreat of the Pleistocene glaciers and the reinvasion of northern New York State *N. chittenangoensis* could have diverged relatively recently from *N. ovalis* in occupying the falls. Overall, there is such great congruency among the results of the anatomical and genetic data sets that we can use the anatomical data to conclude that *N. ovalis* and *N. chittenangoensis* are distinct species.

The situation for the two populations of *Novisuccinea* from Minnesota is the opposite of that of *N. ovalis* and *N. chittenangoensis.* There are so few anatomical differences between the populations that with a morphological similarity coefficient of 0.843, we at first considered them conspecific. The genetic data, by contrast, showed a considerable amount of divergence, i.e. D= 0.143. Combining the data sets, one could consider the populations to be either subspecies or species. The conservative decision is to consider them subspecies until more is known about these and other regional populations, although there are shell morphological differences between the two populations.

In summary, for the Succineidae, morphological and electrophoretic data are generally congruent. However, there are cases where there is little morphological differentiation but considerable genetic divergence between some populations and vice-versa. When beginning a study there is no a priori way of knowing what one will find. Electrophoretic data are of great value in many cases in helping one uncover cryptic species. Coupling morphological and molecular genetic data, one can resolve most problems encountered in a systematic study such as this. Shell morphological data provide the poorest evidence of species identity in the Succineidae; although body pigment patterns and some shell characters are diagnostic, variation in shell shape within populations is often as great as variation between species.

Zoogeography

Riexinger et al. (1983) searched 14 waterfalls in central and western New York State without finding other populations of *Novisuccinea chittenangoensis*. Hubricht (1985), however, listed *N. chittenangoensis* from widely-scattered areas including Iowa, West Virginia, and New York. Some of Hubricht's specimens are now housed at The Academy of Natural Sciences. His lot #47434 (ANSP 362984) from Spruce Knob, West Virginia, is not *N. chittenangoensis*, in our opinion, although it might well be in the *Novisuccinea ovalis* group. It is small and has a low spire. Hubricht's subfossil or fossil specimens from St. Louis County, Missouri, and Madison and St. Clair counties, Illinois (ANSP 363009-363011) do look quite similar to *N. chittenangoensis*, but species-level identification cannot be made on shell material, and there are subtle shell differences between these specimens and the Chittenango population. Grimm (1981) listed several Pleistocene and post-Pleistocene deposits containing *N. chittenangoensis*, from Arkansas to SW Ontario. He synonymized *N. chittenangoensis* with *N. o. pleisotocenica* Baker (1927). He reported four other living colonies besides that at Chittenango Falls: Hubricht's locality in West Virginia, a locality in Virginia near the Clinch River collected by Arthur Clark, an island near Montreal collected by Fowler, and Stratton Gap collected by both Hubricht and Grimm. The habitats of all four localities differ from Chittenango Falls. The West Virginia locality is a mountain pass, and specimens collected there did not have the black mantle marking characteristic of *Novisuccinea ovalis* and *N. chittenangoensis*. The Virginia locality was near a mountain stream. None of these are near waterfalls or are as damp as the Chittenango Falls locality.

Succinea putris Linné, 1758, has been reported at several localities in North America. Hubricht (1985) synonymized *S. pennsylvanica* Pilsbry, 1948, with it based on shell shape alone and therefore listed *S. putris* from NE Pennsylvania and NW New York. His collections contain specimens from Forest County, PA (ANSP 362993), Tioga County, PA, and Cattaraugus Co., NY (362995). It has yet to be proved that *S. putris* s.s. has been introduced to the United States.

LITERATURE CITED

Aloi, M. A. 1985. Population dynamics of a pulmonate snail adjacent to a central New York stream. Unpublished MS thesis. State University of New York, College of Environmental Science and Forestry. 116 pp.

Aloi, M. A. and N. H. Ringer. 1982. Population biology and density of *Succinea chittenangoensis*. Final contract report to New York State Dept. Environmental Conservation under Federal Aid to Endangered Species Project E-1-7. 27 pp.

Anonymous. 1984. Recovery plans approved for five mollusks. Endangered Species Technical Bulletin, January, 1984, Dept. of Interior, U.S. Fish and Wildlife Service, 9(1): 1.

Ayala, F. J., D. Hedgecock, G. S. Zumwalt, and J. W. Valentine. 1973. Genetic variation in *Tridacna maxima*, an ecological analog of some unsuccessful evolutionary lineages. Evolution 27: 177-191.

Baker, F. C. 1927. Description of new forms of Pleistocene land mollusks from Illinois with remarks on other species. Nautilus 40(4): 114-120.

Brewer, G. J. 1970. An introduction to isozyme techniques. New York: Academic Press, 186 pp.

Cavalli-Sforza, L. L., and A. W. F. Edwards. 1967. Phylogenetic analysis: models and estimation procedures. Evolution 21: 550-570.

Davis, G. M. 1967. The systematic relationship of *Pomatiopsis lapidaria* and *Oncomelania hupensis formosana* (Prosobranchia: Hydrobiidae). Malacologia 6: 1-143.

Davis, G. M. and W. P. Carney. 1973. Description of

Oncomelania hupensis lindoensis, first intermediate host of *Schistosoma japonicum* in Sulawesi (Celebes). Proceedings of The Academy of Natural Sciences of Philadelphia 125(1): 1-34.

Davis, G. M. and G. J. Greer. 1980. A new genus and two new species of Triculinae (Gastropoda: Prosobranchia) and the transmission of a Malaysian *Schistosoma* sp. Proceedings of The Academy of Natural Sciences of Philadelphia 132: 245-276.

Davis, G.M., V.Kitikoon, and P. Temcharoen. 1976. Monograph on *"Lithoglyphopsis" aperta*, the snail host of Mekong River schistosomiasis. Malacologia 15(2): 241-287.

Davis, G. M., Y. H. Kuo, K. E. Hoagland, P. L. Chen, H. M. Yang, and D. J. Chen. 1983. Advances in the systematics of the Triculinae (Gastropoda: Prosobranchia): the genus *Fenonuilia* of Yunnan, China. Proceedings of The Academy of Natural Sciences of Philadelphia 135: 177-199.

Davis, G.M., W. H. Heard, S. L. H. Fuller, and C. Hesterman. 1981. Molecular genetics and speciation in *Elliptio* and its relationships to other taxa of North American Unionidae (Bivalvia). Biological Journal of the Linnean Society 15: 131-150.

Dillon, R. T. and Davis, G. M. 1980. The *Goniobasis* of Southern Virginia and northwestern North Carolina: genetic and shell morphometric relationships. Malacologia 20: 83-98.

Draparnaud, J. P. R. 1801. Tableau des mollusques terrestres et fluviatiles de la France. 116 pp; (pls. 1-13, 1805 revision). Paris.

Emberton, K. 1985. Seasonal changes in the reproductive gross anatomy of the land snail *Triodopsis tridentata tridentata* (Pulmonata: Polygyridae). Malacologia 26(1-2): 225-239.

Franzen, D.S. 1959. Anatomy of *Succinea ovalis* Say. Proceedings of the Malacological Society of London 33(5): 193-199.

Grimm, F.W. 1981. A review of the Chittenango ovate amber snail, *Succinea chittenangoensis*, Pilsbry, 1908 — a Pleistocene relict now greatly restricted in distribution. Contract report to the New York State Department of Environmental Conservation Endangered Species Unit. 30 pp.

Harris, S. A. and L. Hubricht. 1982. Distribution of the species of the genus *Oxyloma* (Mollusca, Succineidae) in Southern Canada and the adjacent portions of the United States. Canadian Journal of Zoology 60(7): 1607-1611.

Hubricht, L. 1972. Endangered land snails of the Eastern United States. Sterkiana 45: 33.

Hubricht, L. 1983. Five new species of land-snails from the southeastern United States with notes on other species. Gastropodia 2: 13-19.

Hubricht, L. 1985. The distributions of the native land mollusks of the Eastern United States. Fieldiana, Zoology, New Series, No. 24: 191 pp.

Lea, I. 1834. Observations on the Naïades; and descriptions of new species of that and other families. Second Supplement. Transactions of the American Philosophical Society, New Series 5(1): 95-117.

Lewontin, R. C. 1974. The Genetic Basis of Evolutionary Change. New York: Columbia University Press, 346 pp.

Nei, M. 1972. Genetic distance between populations. American Naturalist 106: 283-292.

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583-590.

Patterson C. M. 1971. Taxonomic studies of the land snail family Succineidae. Malacological Review 4: 131-202.

Pilsbry, H. A. 1908. Notes on *Succinea ovalis* Say and *S. obliqua* Say. Proceedings of The Academy of Natural Sciences of Philadelphia 60: 45-51, plate 7.

Pilsbry, H. A. 1948. Succineidae. *In:* Land Mollusca of North America (North of Mexico). Monographs of the Academy of Natural Sciences of Philadelphia No. 3, Vol. 2, part 2: 771-847.

Poulik, M. D. 1957. Starch gel electrophoresis in a discontinuous system of buffers. Nature 180: 1477-1479.

Quick, H. E. 1933. The anatomy of British Succineae. Proceedings of the Malacological Society of London. 20: 295-318, pls. 23-25.

Riexinger, P., J. Proud, T. Lyons, and D. Sulitka. 1983. Chittenango ovate amber snail recovery plan. Region 5 U.S. Fish and Wildlife Service Report, in cooperation with the Chittenango Ovate Amber Snail Recovery Team. March 24, 1983. Fish and Wild Life Reference Service, Unit i. Denver, Colorado.

Rigby, J. E. 1965. *Succinea putris:* A terrestrial opisthobranch mollusc. Proceedings of the Zoological Society of London. 144:445-486.

Rogers, J. S. 1972. Measures of genetic similarity and genetic distance. Studies in Genetics, VII. The University of Texas Publication No. 7213, 145-153.

Rohlf, F. J., J. Kishpaugh, and D. Kirk. 1972. NT-

SYS: Numerical taxonomy system of multivariate statistical programs. Technical Report, State University of New York, Stony Brook.

Say, T. 1817. Description of seven species of American fresh water and land snails, not noticed in the system. Journal of the Academy of Natural Sciences of Philadelphia 1: 13-16.

Shaw, R. S. and Prasad, R. 1970. Starch gel electrophoresis of enzymes -- a compilation of recipes. Biochemical Genetics 4: 297-320.

Solem, A. 1976. Status of *Succinea ovalis chittenangoensis* Pilsbry, 1908. Nautilus 90(3): 107-114.

Solem, A. 1981. Camaenid land snails from western and central Australia (Mollusca: Pulmonata: Camaeniidae). II. Taxa from the Kimberley, Amplirhagada Iredale, 1933. Records of the western Australian Museum, Supplement 11: 147-320.

Swofford, D. L. and R. B. Selander. 1981. Biosys-1. A computer program for the analysis of allelic variation in genetics. Release 1. User's Manual. University of Illinois at Urbana-Champaign, Urbana, Ill. 65 pp.

Thomeé, E. 1986. Behavioral ecology of the endangered Chittenango ovate amber snail Succinea chittenangoensis and a sympatric introduced succineid. Unpublished ms thesis. State University of New York, College of Environmental Science and Forestry. 227 pp.

Thomeé, E.T. and D. L. Dindal. 1984. Community ecology and behavior of an endangered species of snail, *Succinea chittenangoensis.* Interim Report to Endangered species Unit, New York State Department of Environmental Conservation, Delmos, New York, 37 pp.

Tracy, M. L., N. F. Bellet, and C. D. Graven. 1975. Excess allozyme homozygosity and breeding population structure in the mussel *Mytilus californianus*. Marine Biology 32: 303-311.

Villalobos-Dominquez, C. and J. Villalobos. 1947. Atlas de los Colores. Buenos Aires: Liberia el Atenco Editorial, 74 p.

Westerlund, C. A. 1855. Fauna der in der Paläarctischen Region. Binnen conch. 5: 1-135.

Appendix Table 1. Allele frequencies involving 23 loci, 3 genera, 8 species, and 11 populations.

	Population										
	N. oval.	*N. chit.*	*S. sp. B*		*S. cf. penn.*	*O. ret.*		*O. dec.*	*N. sp. A*		*S. sp. C*
	Sullivan	Falls	Falls	Cress		Fenner	Sullivan		Minn. A	Minn. B	Wiss.
PEPT1											
(N)	15	14	11	16	15	16	79	16	10	10	26
A	1.000	1.000	0	0	0	1.000	0.987	1	0	0.25	0.0
B	0	0	1.000	1.000	1.000	0.0	0.013	0	0	0	1.000
C	0	0	0	0	0	0	0	0	1.000	0.75	0
PEPT2											
(N)	15	14	8	13	1	16	79	16	10	10	12
A	0	0	0	0	0	0	0	0.0	0	0	0
B	0	0	0.313	0.231	1.000	1.000	0.867	1.000	0	0	1.000
C	1.000	1.000	0.688	0.769	0	0	0.133	0.0	1.000	1.000	0
PEPG3											
(N)	15	14	9	16	15	11	79	16	10	10	26
A	1.000	1.000	0	0	0	0	0	0.0	0	0.300	0.231
B	0	0	0	0	0	1.000	1.000	1.000	0	0	0
C	0	0	1.000	1.000	1.000	0	0	0.0	1.000	0.700	0.769
D	0	0	0	0	0	0	0				
EST-1											
(N)	15	14	6	3	15	6	16	3	10	10	26
A	0	0	1.000	1.000	1.000	1.000	1.000	1.000	0	0	1.000
B	1.000	1.000	0	0	0	0	0	0.0	1.000	1.000	0.0
EST-3											
(N)	15	14	9	16	15	16	79	16	10	10	26
A	0	0	1.000	1.000	0	0	0	0	0	0.050	0
B	0.800	0.893	0	0	0	0	0	0.0	1.000	0.950	0
C	0	0	0	0	0	0	0	1.000	0	0	0
D	0	0	0	0	0	1.000	1.000	0	0	0	0
E	0.200	0.107	0	0	1.000	0	0	0	0	0	1.000

Appendix Table 1 continued

EST-4											
(N)	15	13	11	16	15	5	51	6	10	10	26
A	0	0.038	0	0	0.867	1.000	0.392	0	0	0	0.058
B	0.800	0.692	1.000	0.938	0	0	0	0	0	0	0.423
C	0.200	0.269	0.0	0.063	0.133	0	0.608	1.000	1.000	1.000	0.519
LAP											
(N)	4	9	11	13	15	11	39	3	10	10	26
A	0	0	0.045	0	0	0	0	0	0	0	0.058
B	0	0	0.955	1.000	0.900	0	0	0	0	0	0.750
C	0	0.056	0	0	0	0	0.051	1.000	1.000	0	0.192
D	0.75	0.556	0	0	0	0	0	0	0	0	0
E	0.25	0.389	0	0	0	1.000	0.949	0	0	0	0
F	0	0	0	0	0	0	0	0	0	1.000	0
G	0	0	0	0	0.100	0	0	0	0	0	0
ISDH2											
(N)	15	14	7	9	6	16	79	16	10	10	1
A	0	0	1.000	1.000	0	0	0	0	0	0	1.000
B	1.000	1.000	0	0	0	0	0	0.0	1.000	1.000	0
C	0	0	0	0	0	1.000	1.000	1.000	0	0	0
D	0	0	0	0	1.000	0	0	0	0	0	0
GPI											
(N)	14	14	11	16	15	16	79	16	10	10	26
A	0.143	0.179	0	0	0.033	0.031	0.013	0	1.000	1.000	0.192
B	0.857	0.821	0	0	0	0.719	0.835	0	0	0	0
C	0	0	1.000	1.000	0.967	0	0	0	0	0	0.808
D	0	0	0	0	0	0	0.006	0	0	0	0
E	0	0	0	0	0	0.250	0.146	1.000	0	0	0
AGPD2											
(N)	15	14	11	16	15	16	79	16	10	10	26
A	0	0	1.000	1.000	0	1.000	1.000	1.000	0	0	0
B	1.000	1.000	0	0	0	0	0	0	1.000	1.000	0
C	0	0	0	0	1.000	0	0	0	0	0	0
AAT-1											
(N)	15	14	11	16	6	16	79	6	10	10	12
A	0	0	1.000	1.000	1.000	1.000	1.000	1.000	0	0.100	1.000
B	1.000	1.000	0	0	0	0	0	0.0	1.000	0.900	0

Appendix Table 1 continued

AAT-2											
(N)	14	14	11	16	6	16	79	13	10	10	12
A	0.143	0	0	0	0	1.000	1.000	1.000	0	0	0
B	0	0	1.000	1.000	1.000	0	0	0	0	0.200	1.000
C	0.857	1.000	0	0	0	0	0	0	1.000	0.800	0
MPI											
(N)	15	14	11	16	15	16	79	16	10	10	26
A	0	0	0	0	0.033	1.000	1.000	1.000	0	0	0.038
B	0	0	1.000	1.000	0.767	0	0	0	0	0	0.962
C	1.000	1.000	0	0	0	0	0	0	1.000	1.000	0
D	0	0	0	0	0.200	0	0	0	0	0	0
6PGD											
(N)	15	14	11	16	15	16	78	16	10	10	26
A	0	0	1.000	1.000	0	0	0	0	0.650	0	0.077
B	0	0	0	0	0	0	0	0	0	0	0
C	1.000	1.000	0	0	0	1.000	1.000	1.000	0.35	1	0
D	0	0	0	0	1.000	0	0	0	0	0	0.923
SDH											
(N)	15	14	11	16	15	16	58	6	10	10	26
A	0	0	0	0	0	1.000	1.000	1.000	0	0	0
B	0	0	1.000	1.000	0	0	0	0	0	0	1.000
C	1.000	1.000	0	0	0	0	0	0	1.000	1.000	0
D	0	0	0	0	1.000	0	0	0	0	0	0
PGM-1											
(N)	15	14	11	16	15	16	79	16	10	10	26
A	0.133	0.214	0	0	0	0	0	0	1.000	0.200	0
B	0.767	0.643	0	0	0	0	0	0	0	0.650	0
C	0.100	0.143	0.773	0.844	0.700	0	0	0	0	0	0.519
D	0	0	0.227	0.156	0.300	1.000	1.000	1.000	0	0	0.481
E	0	0	0	0	0	0	0	0	0	0.150	0
G6PD											
(N)	15	14	9	16	15	16	56	5	10	10	26
A	0	0	0	0	0	1.000	1.000	0.100	0	0	0
B	1.000	1.000	0	0	0	0	0	0	0	0	0
C	0	0	1.000	1.000	0	0	0	0	0	0	1.000
D	0	0	0	0	0	0	0	0.900	0	0	0
E	0	0	0	0	1.000	0	0	0	1.000	1.000	0

Appendix Table 1 continued

SOD											
(N)	15	14	11	16	9	16	79	16	10	10	26
A	1.000	1.000	0	0	0	0	0	0	1.000	1.000	0
B	0	0	0	0	0	1.000	1.000	1.000	0	0	0
C	0	0	0	0.094	0.667	0	0	0	0	0	0
D	0	0	1.000	0.906	0.333	0	0	0	0	0	1.000
AO											
(N)	14	10	11	16	6	16	79	16	10	10	12
A	1.000	1.000	0	0	0	0	0	0	1.000	1.000	0.75
B	0	0	1.000	1.000	1.000	0	0	0	0	0	0.25
C	0	0	0	0	0	1.000	1.000	1.000	0	0	0
MDH-1											
(N)	14	14	11	16	15	16	79	8	10	10	26
A	0	0	0	0	0	1.000	1.000	1.000	0	0	0
B	0	0	1.000	1.000	1.000	0	0	0	0	0	1.000
C	0.964	1.000	0	0	0	0	0	0	1.000	1.000	0
D	0.036	0	0	0	0	0	0	0	0	0	0
MDH-2											
(N)	13	11	11	16	15	16	54	6	10	10	26
A	0.077	0.045	0	0	0	0	0	0	1.000	1.000	0
B	0	0	0	0	0	1.000	1.000	0.583	0	0	0
C	0.923	0.955	0	0	0	0	0	0.417	0	0	0.096
D	0	0	1.000	1.000	0	0	0	0	0	0	0.019
E	0	0	0	0	1.000	0	0	0	0	0	0.885
ACPH											
(N)	15	14	11	16	6	16	79	16	10	10	12
A	0	0	1.000	1.000	1.000	1.000	1.000	1.000	0	0	1.000
B	1.000	1.000	0	0	0	0	0	0	1.000	1.000	0
HEX-2											
(N)	12	6	7	10	15	11	58	7	10	10	25
A	0	0	0	0	0	1.000	1.000	1.000	0	0	0
B	0	0	0	0	0	0	0	0	0	0	0
C	1.000	1.000	0	0	0	0	0	0	1.000	1.000	0
D	0	0	1.000	1.000	1.000	0	0	0	0	0	0.86
E	0	0	0	0	0	0	0	0	0	0	0.14

Appendix Table 2. Genetic variability at 23 loci for all populations. The standard errors in [ ].

Population		Mean sample size per locus	Mean No. alleles per locus	Percentage loci polymorphic*	Mean Heterozygosity	
					Direct-Count	HDYWBG Expected**
Novisuccinea						
chit.	Falls	13.1 [0.4]	1.4 [0.2]	26.1	0.005 [0.024]	0.094 [0.039]
ovalis	Sullivan	14.1 [0.5]	1.4 [0.1]	34.8	0.075 [0.031]	0.096 [0.032]
sp. A	Minn. A	10 [0]	1 [0]	4.3	0.004 [0.004]	0.021 [0.02]
sp. A	Minn. B	10 [0]	1.3 [0.1]	26.1	0.039 [0.023]	0.087 [0.035]
Succinea						
cf. penn.	Watercress	12.2 [0.9]	1.3 [0.1]	26.1	0.044 [0.018]	0.077 [0.032]
sp. B	Falls	10 [0.03]	1.1 [0.1]	13	0.021 [0.013]	0.04 [0.025]
sp. B	Watercress	14.6 [0.7]	1.2 [0.1]	17.4	0.035 [0.019]	0.041 [0.021]
sp. C	Wissahicken	21.8 [1.5]	1.6 [0.2]	43.5	0.069 [0.023]	0.14 [0.04]
Oxyloma						
retusa	Fenner	14.4 [0.7]	1.1 [0.1]	4.3	0.019 [0.019]	0.019 [0.019]
retusa	Sullivan	69.3 [3.5]	1.3 [0.1]	21.7	0.025 [0.012]	0.049 [0.025]
decampi	Falls	11.8 [1.1]	1.1 [0.1]	8.7	0.160 [0.011]	0.032 [0.024]

*Locus is considered polymorphic if more than one allele was detected **Unbiased estimate (see Nei, 1978).

Proceedings of the Academy of Natural Sciences of Philadelphia 138: 527-532, 1987

Virginia Orr Maes (1920-1986): Biography and Malacological Bibliography

ROBERT ROBERTSON

The Academy of Natural Sciences of Philadelphia
19th and the Parkway, Philadelphia, PA 19103

Virginia Orr Maes at an American Malacological Union meeting
(Key West, Florida, July 17, 1970). Photo R. Robertson.

INTRODUCTION. Virginia Orr Maes, a first-rate and world-famous marine malacologist associated with The Academy of Natural Sciences of Philadelphia (ANSP) since the early 1950's, died of cancer at the age of 65 on October 24, 1986. She last worked at her beloved ANSP about ten days earlier.

EARLY YEARS, YOUTH, AND COLLEGE. Virginia, who was also known to some friends as Dinty, was born in Philadelphia on December 26, 1920. She grew up in the large Orr family home (Willowbrook), near Paoli, on the Main Line, W.N.W. of Philadelphia. Virginia graduated from Baldwin School, Bryn Mawr, Pennsylvania, in 1938. From 1938 to 1940 she attended Wellesley College, Massachusetts, but did not graduate—showing in retrospect how unnecessary a higher degree can be. During World War II, Virginia aided the United States war effort by working in a factory.

INTERESTS. At various times in her life, Virginia enjoyed sailing, horseback riding, birdwatching, fishing, gardening, pets (cats, dogs, and a donkey), baseball, playing the flute, and choral singing. She especially liked Bach cantatas and Brahms' German Requiem.

Virginia kept home weather records. She disliked winter, and tried whenever possible to travel to warmer places where she could collect mollusks well away from snow and ice.

Photography was one of Virginia's skills. Some of her early natural history photographs were published in *Frontiers*, ANSP's popular magazine. She taught me photography.

Virginia's interest in malacology was sparked by a geology course given in the early 1950's by John Dyas Parker (1915-1977), long-time assistant to the great ANSP malacologist Henry A. Pilsbry (1862-1957).

ASSOCIATIONS WITH ANSP. Virginia first volunteered and later became a paid Scientific Assistant in the Department of Mollusks (as the Department of Malacology was then called) in 1955, working first with Pilsbry, and then with Dr. R. Tucker Abbott (1919-) when he came to ANSP in 1954. She received guidance and informal malacological training primarily from Abbott. Upon her marriage to Robert A. Maes in 1963, Virginia gave up her small salary and became Research Associate, faithfully coming into ANSP three days a week. In 1970 she was appointed Research Fellow, the position she held until her demise. Virginia was the departmental historian and it is a great pity that she did not publish on this topic. She did, though, leave notes and a big chronological scroll from a talk she gave at a Philadelphia Shell Club meeting in 1974.

MALACOLOGY AT ANSP DURING THE LATE 1950'S AND 1960'S. In the mid-1950's, the wealthy, shell-collecting businessman Alfred J. Ostheimer, III (1908-1983) began giving support for a research program in the systematics of shallow-water, tropical Indo-Pacific marine mollusks. The Natural (not National!) Science Foundation and the Pilsbry Chair of Malacology were created, and Tucker Abbott came to Philadelphia from the Smithsonian Institution to head the program. In 1959 the monographic serial *Indo-Pacific Mollusca* began publication.

EXPEDITIONS. The Natural Science Foundation sponsored numerous expeditions to collect mainly Indo-Pacific mollusks. As a result, ANSP now has the largest and best Indo-Pacific collection of any museum in the world. Virginia helped substantially to bring this about. Ostheimer had a large yacht, the Gloria Maris (named after the famous once-rare shell *Conus gloriamaris*), that was used for several of the expeditions in the western Pacific. Virginia's first major malacological field experiences were in South Africa (Table 1). Subsequently, she collected on many of the expeditions, including those on the Gloria to the Palaus and the then Dutch New Guinea. Her field companions included George F. (1907-1970) and Mary Clapp Kline. Virginia struck up a special friendship with the New Zealand malacologist, the late A. W. B. Powell, and they collected together from the Gloria and in New Zealand. Ostheimer's first wife Ruth E. M. Ostheimer and Virginia went to Cocos-Keeling as part of the U.S. Program in Biology, International Indian Ocean Expedition (1963). After her marriage, Virginia went mainly on shorter trips to the American tropics. Her last expedition was, however, to Christmas Island in the central Pacific, where she spent a Christmas with her husband. Altogether, Virginia's collecting netted ANSP more than 25811 lots (Table 1), 7% of the entire (380,537-lot) ANSP mollusk collection.

CURATION. Virginia was a first-rate curator (although she never had that title), processing efficiently the huge collections from the Indo-Pacific and elsewhere (5145 lots from Dutch New Guinea!). Her well researched and neatly written identifications and labels are throughout the ANSP collection. Her identifications for outsiders brought to ANSP many specimens—especially turrids. Through Virginia's efforts the ANSP Recent world-wide turrid collection is unquestionably the best in the world.

RESEARCH AND PUBLICATIONS. Virginia was proud of being an "amateur" malacologist. Being under no compulsion to publish or perish, she authored just a few papers, all of them good to excellent. She published twelve malacological research papers, and ten 1- or 2-page abstracts (most of which were followed up by full-length papers).

Virginia was a modern-day naturalist. Throughout her malacological career, she was more interested in the living animals than in just their shells. Her earliest malacological interest was given as "Radulae of marine snails." At Broome, Western Australia, she made "an attempt . . . to collect data as well as shells" (1960b).

Virginia became interested in the marine mollusk faunas of the places where she collected. She chose to publish only on the Cocos-Keeling mollusk fauna (1967a). Early on, Virginia used shell and radula characters in systematic studies of neogastropods such as *Burnupena* (1956b), *Mitromorpha* (1959a), *Engina* (1962a), and *Pleuroploca* (1967b). This led to her discovery of sexually dimorphic radulae in the muricid genus *Nassa* (1966).

Virginia was also much interested in chitons ("kittens" as she called them), but published only one abstract on these (1961) other than the paper by Robertson & Orr (1961).

In her field work in Zanzibar, Virginia observed much shell size and shape variation in *Cypraea annulus* (1959b). She used biometry to show that these populations (ecotypes?) differ as much as do the supposed geographical subspecies of this cowrie recognized by the Schilders.

In her field work in New Caledonia, Virginia discovered a *Capulus*, the egg capsule-brooding females of which make a hole by means unknown through a host scallop's shell (1962b). These females apparently steal some of the food collected by the scallop's ctenidia and passed by the palps to the mouth. The hole in the shell is near the scallop's mouth. The *Capulus* is protandric and males do not make holes. The egg capsules under females perhaps obstruct filter feeding by this *Capulus*.

In her later years, Virginia's publications became fewer and more sophisticated. This can be seen in her work on *Thala* (1975, co-authored with Dorothy Raeihle), in which she combined systematics (shells, radulae, and soft anatomy studied by dissection and histology), life history, and ecology to give a well-rounded account of this mitriform gastropod's biology. She used scanning electron microscopy (SEM) for studying and illustrating its protoconch and radula. Virginia found that *Thala*'s venom is effective on external contact with the skin of its prey, i.e the venom is not injected as is the case in *Conus*.

After her work on *Thala*, Virginia directed all her research efforts towards that most systematically-difficult family Turridae (in which there are about 27,000 scientific names!). In 1983, she published on nine shallow water turrid species living with or near each other in the same habitat in the British Virgin Islands, treating their systematics (shells, radulae, soft anatomy and histology (especially foreguts as these relate to feeding), ecology, and life histories. She documented the identity of some of the polychaete and sipunculid prey.

Towards the end of her life, Virginia was working on a major paper on the shell structures of turrid subfamilies, making thin-sections and fracturing shells and using a SEM. She was finding that each subfamily has its own kind of shell structure. Each of her new research topics presented major new challenges.

Virginia disliked nomenclature ("lawyer work" as she called it). Part of her research credo was not to name any new taxa, there being a surfeit of names in most of the groups on which she worked.

POPULARIZATION. Virginia wrote accounts of four of her collecting trips—South Africa (1956a), Zanzibar (1958), Western Australia (1960c), and Cocos-Keeling (1963), all based on talks. She also published a general article introducing mollusks (1960d).

MEMBERSHIPS. Virginia was a Charter Member of the Philadelphia Shell Club (1955). She was also a member of the American Malacological Union since 1954 (in 1961-1962, she was a Councillor-at-large). Almost every year she spoke at meetings of each group. She also belonged to the West Palm Beach Shell Club. In

1972, Virginia was one of the founders of the Council of Systematic Malacologists (Solem 1973). After 1976, Virginia was a Full Member of Sigma Xi, the Scientific Research Society.

HONORS. Virginia has one genus, six species and, one subspecies of mollusk named for her, all of them gastropods:

Taheitia orrae Turner, 1959: 186-188, pl. 31, figs. 1-2, pl. 32, figs. 1-5. Biak, Dutch New Guinea [Irian Barat, Indonesia]. Holotype ANSP 223656. Truncatellidae (terrestrial).

Strombus urceus subspecies *orrae* Abbott, 1960: 66-67, pl. 20, fig. 28, pl. 41, fig. 5, Augustus Island, Western Australia. Holotype ANSP 247756. Strombidae.

Maesiella McLean in McLean & Poorman, 1971: 102; McLean, 1971: 123. Type species (original designation): *Maesiella maesae* McLean & Poorman, 1971. Turridae.

Maesiella maesae McLean & Poorman, 1971: 101-102, 123, fig. 29. First cove north of Saladita Cove, near Guaymas, Sonora, Mexico.

Pugnus maesae Roth, 1972: 106-107, fig. 1. One mi. N. of Tanjong Puji, West Island, Cocos-Keeling Islands. Holotype ANSP 288324. Marginellidae? If valid, apparently the only marine mollusk species thought to be endemic to Cocos-Keeling.

Simnia maesae Cate, 1973: 71-72, fig. 159. Broome, Roebuck Bay, Western Australia. Holotype Mus. Comp. Zool., Harvard Univ. "No. Acc. 812." [280459] Ovulidae.

Fusiturricula maesae Rios, 1985, p. 133, pl. 46, fig. 604. Off Rio de Janeiro to São Paulo [Brasil]. Turridae.

Anarithma maesi Drivas & Jay, 1986: 9, fig. (color). Réunion [Indian Ocean]. "The holotype will be deposited in the Museum d'Histoire Naturelle in Paris." Turridae.

LATER YEARS. Virginia's 1963 marriage to Robert A. Maes, a foundation director and investment consultant, was most happy, though they had no children. They lived in a country house in Glenmoore, Chester County, Pennsylvania. They traveled frequently, and sometimes fished, hunted birds, and collected mollusks together.

Virginia was intensely loyal to ANSP and a good friend to many of her malacological and non-malacological acquaintances around the world. She will be remembered for, among other things, her delightful humor, her common sense, her carefully chosen spoken and written words, her generosity, and her malacological expertise. Characteristically, the day before her early winter death, plucky Virginia was planting crocuses and chatting with a niece.

LEGACY. In memory of his wife, Robert Maes has established at ANSP the Virginia Orr Maes Memorial Fund with a gift of $100,000. Together with many donations received in her memory from friends and colleagues, this endowment fund will provide support for continued work in malacology.

ACKNOWLEDGMENTS

Dr. R. Tucker Abbott was very helpful with information and advice. Carol Spawn, ANSP Manuscript/Archives Librarian and presently Acting Head Librarian, gave useful criticisms of an earlier draft. Dr. Kenneth C. Emberton helped with Table 1. Dr. Arthur E. Bogan and Gary Rosenberg saved me from some embarrassing commissions and omissions.

MALACOLOGICAL BIBLIOGRAPHY
as "V. ORR"

1956a. Sea shelling safari [to South Africa]. Proceedings of the Philadelphia Shell Club 1(1): 10-12 (Sept.).

1956b. The South African gastropod genus *Burnupena* (Buccinidae). Proceedings of the Academy of Natural Sciences of Philadelphia 108: 249-263, pls. 19-20 (Dec. 21).

1958. Molluscan road to Zanzibar. Proceedings of the Philadelphia Shell Club 1(3): 1-3 (Oct.).

1959a. Classification and radula of *Mitromorpha atramentosa*. Nautilus 72: 75-78 (Jan. 15).

1959b. A bionomic shell study of *Monetaria annulus* (Gastropoda: Cypraeidae) from Zanzibar. Notulae Naturae of the Academy of Natural Sciences of Philadelphia no. 313: 11 pp., 2 pls. (May 29).

1960a. Observations of *Murex stainforthi* and *M. monodon*. American Malacological Union ... Annual Reports for 1959 [Bulletin 26], pp. 13-14. Abstract. (Jan. 1).

1960b. Collecting at Broome, Western Australia. American Malacological Union ... Annual Reports for 1959 [Bulletin 26], pp. 23-24. Abstract. (Jan. 1). See 1960c.

1960c. Expedition to Western Australia. Proceedings of the Philadelphia Shell Club 1(4): 9-12 (April).

1960d. Clams, squids and other mollusks. Foote Prints (Foote Mineral Co., Philadelphia) 31(2): 3-11.

1961. Some South African ischnochitons. American Malacological Union ... Annual Reports for 1960 [Bulletin 27], pp. 16-17. Abstract. (Jan. 1).

1962a. Type of the genus *Engina* (Buccinidae). Nautilus 75: 107-109, pl. 10. (Jan. 9).

1962b. The drilling habit of *Capulus danieli* (Crosse)(Mollusca: Gastropoda). Veliger 5: 63-67, pl. 7. (Oct. 1).

1962c. Shell-boring habit of *Capulus danieli* (Crosse). American Malacological Union. Annual Reports for 1962 [Bulletin 29], p. 10. Abstract. (Dec. 1). See 1962b.

1963. Collecting on Cocos-Keeling, Indian Ocean. American Malacological Union. Annual Reports for 1963 [Bulletin 30], pp. 3-4. Abstract. (Dec. 1). See 1967a.

AS "V. ORR MAES"

1965. Sexual dimorphism in the radula of the muricid genus *Nassa*. American Malacological Union. Annual Reports for 1965 [Bulletin 32], pp. 16-17. Abstract. (Dec. 1). See 1966.

1966. Sexual dimorphism in the radula of the muricid genus *Nassa*. Nautilus 79: 73-80 (Jan. 25).

1967a. The littoral marine mollusks of Cocos-Keeling Islands (Indian Ocean). Proceedings of the Academy of Natural Sciences of Philadelphia 119: 93-217 (Sept. 6).

1967b. Radulae of two species of *Pleuroploca* (Fasciolariidae) from the Indo-Pacific. Nautilus 81: 48-54 (Oct. 16).

1971. Evolution of the toxoglossate radula and methods of envenomation. American Malacological Union. Annual Reports for 1970 [Bulletin 37], pp. 69-72. (Feb. 18).

1976. The genus *Pilsbryspira*: its position in history and the family Turridae. Bulletin of the American Malacological Union, Inc. for 1975, pp. 60-61. Abstract. (Jan. 30).

1979. Estimating the size of small gastropods for comparative purposes. Bulletin of the American Malacological Union for 1979, p. 62. Abstract. (1980?).

1980. Food of a West Indian turrid assemblage. Bulletin of the American Malacological Union for 1980, p. 76. Abstract. (1981?). See 1983.

1981. Protoconchs past and present: a comparison of some fossil Turridae with their western Atlantic and eastern Pacific descendents. Bulletin of the American Malacological Union for 1981, 31. Abstract. (1982?).

1983. Observations on the systematics and biology of a turrid gastropod assemblage in the British Virgin Islands. Bulletin of Marine Science 33: 305-335.

Maes, Virginia Orr & Dorothy Raeihle

1975. Systematics and biology of *Thala floridana* (Gastropoda: Vexillidae). Malacologia 15: 43-67 (Dec. 18).

Robertson, Robert & V. Orr

1961. Review of pyramidellid hosts, with notes on an *Odostomia* parasitic on a chiton. Nautilus 74: 85-91, pl. 6 (Jan. 11).

Other literature cited or consulted

Abbott, R.T. 1960. The genus *Strombus* in the Indo-Pacific. Indo-Pacific Mollusca 1 (2): 33-146.

Abbott, R.T. (editor-in-chief). 1973. American malacologists; a national register of professional and amateur malacologists and private shell collectors, and biographies of early American mollusk workers born between 1618 and 1900. Ed. 1. American Malacologists, Falls Church, Virginia, iv + 494 pp.

Abbott, R.T. (editor). 1987. Register of American malacologists. Ed. 2. American Malacologists, Melbourne, Florida, and Burlington, Massachusetts, xiii + 168 pp.

Cate, C.N. 1973. A systematic revision of the Recent cypraeid [sic] family Ovulidae (Mollusca: Gastropoda). Veliger 15 suppl.: iv + 116 pp., 51 pls. (4 in color).

Drivas, J. & M. Jay. 1986. Shells of Réunion. 8 - Family Turridae Swainson, 1840. La Conchiglia, Year 18, nos. 208-209, pp. 8-10, 11 figs.

McLean, J. H. 1971. A revised classification of the family Turridae, with the proposal of new subfamilies, genera, and subgenera from the eastern Pacific.

Veliger 14: 114-130.
McLean, J. H. & R. Poorman. 1971. New species of tropical eastern Pacific Turridae. Veliger 14: 89-113.
Rios, E. C. 1985. Seashells of Brazil. Rio Grande do Sul, 329 pp., 102 pls.
[Robertson, R.] 1987. In memoriam [Virginia Orr Maes]. Academy News 10(1): 3, photo.
Roth, B. 1972. A new species of *Pugnus* from Cocos-Keeling Islands, Indian Ocean (Gastropoda). Bulletin of the Southern California Academy of Sciences 71: 106-107.
Solem, [G.] A. 1973. Council of Systematic Malacologists, Malacological Review 6: 73.
Turner, R. D. 1959. Notes on the genus *Taheitia* (Truncatellidae) in New Guinea with the description of a new species. Occasional Papers on Mollusks (Department of Mollusks, Museum of Comparative Zoology, Harvard University) 2: 181-188.

Table 1. Years and places where Virginia Orr Maes collected 20 or more lots of mainly marine mollusks, and total resulting lots cataloged into the ANSP collection (alcohol as well as dry lots). On many of these trips, Virginia collected in company with other people; her counts and their counts cannot be separated. Duplicate lots used for exchanges with other museums and persons were not counted. The sources of information were the ANSP Malacology collection catalogs, logbooks and other manuscript sources.

Years	Places	Nos. lots
1953	South Africa	21
1955	South Africa (again)	701
1955	Palau	4200
1956	Dutch New Guinea	5145
1957	Zanzibar	2454
1958	Broome, W. Australia	1334
1960	Mauritius	1310
1960	W. Australia (again)	181
1960 - 1961	New Caledonia	3129
1961	New Zealand	201
1963	Barbados	147
1963	Cocos-Keeling	1794
1963	Society Islands	50
1964	Cayman Brac	323
1965	Grand Bahama	180
1965	Isla Mujeres	147
1965	Ireland	21
1966	Grenada	1731
1967	Guadeloupe	130
1970	Bonaire	103
1972	St. Vincent	165
1973-1979	Brit. Virgin Islands (4 visits)	419
1975	Mexico	29
1979	Texas	197
1980	Barbuda	237
1983	Costa Rica	443
1983	Ecuador	191
1983	Mexico (Pacific)	186
1983	Panama	491
1985	Christmas Island (Pacific)	151
	Total no. lots	25,811

THE ACADEMY OF NATURAL SCIENCES OF PHILADELPHIA
MONOGRAPHS

		U. S Canada	Other
1.	The Scrophulariaceae of Eastern Temperate North America. Frances W. Pennell. November 1935. 650 pp.	13.00	15.50
2.	The Fishes of the George Vanderbilt Pacific Expedition, 1937. Henry W. Fowler. 1938. 349 pp.	23.00	25.50
3.	Land Mollusca of North American (North of Mexico). Henry A. Pilsbry. 1939-1948. (Two volumes. Four parts). 573, 418, 520 and 592 pp., respectively. Price per part	50.00	52.50
4.	Australian Blattidae of the subfamilies Chorisoneurinae and Ectobiinae (Orthoptera). Morgan Hebard. April 1943. 129 pp.	12.00	14.00
5.	The Scrophulariaceae of the Western Himalayas. Francis W. Pennell. September, 1943. 1163 pp.	8.00	10.00
6.	Results of the Figth George Vanderbilt Expedition, 1941 George Vanderbilt et al, 1944. 583 pp.	26.00	28.50
7.	A study of the Fishes of the Southern Piedmont and Coasta plain. Henry W. Fowler, 1945. 408 pp.	26.00	28.50
10.	The flora of the Upper Cretaceous Woodbine Sand in Denton County, Texas. Donald L. MacNeal. June, 1958. 152 pp.	11.00	13.00
12.	A Monograph of the Orthoptera of North America (North of Mexico). James A. G. Rehn and Harold J. Grant, Jr. January 1961. 257 pp.	18.00	20.00
13.	The Diatoms of the United States (exclusive of Alaska and Hawaii). Volume I. Ruth Patrick and Charles W. Reimer. May, 1966. 213 pp.	41.00	43.50
13.	The Diatoms of the United States (exclusive of Alaska and Hawaii). Volume II. Ruth Patrick and Charles W. Reimer. December, 1975.	30.00	32.00
14.	Results of the Catherwood Foundation Peruvian-Amazon Expedition. Ruth Patrick et al., 1966. 495 pp.	23.00	25.50
15.	Revision of the Classification of the Oscillatoriaceae. Frances Drouet. August 1968. 370 pp.	18.00	20.50
16.	A monograph on Plectognath Fishes of the Superfamily Triacanthoidea. James C. Tyler. 1968. 364 pp.	22.00	24.50
17.	The Adults of the Subfamily Tanypodinae (=Pelopiinae) in North America (Diptera: Chironomidae). Selwyn S. Roback. March, 1971. 410 pp.	27.00	29.50
18.	The Ostracod Family Entocytheridae. Dabney G. and C. W. Hart, Jr. October 1974.	27.00	29.50
19.	The Saber-toothed blennies. Tribe Nemophini (Pisces: Blenniidae). William F. Smith-Vaniz. December, 1976. 196pp.	17.00	19.00
20.	The Origin and Evolution of the Gastropod Family Pomatiopsidae, with Emphasis on the Mekong River Triculinae. George M. Davis. June 1979.	14.00	15.50
21.	The Feather Mite Family Eustathiidae (Acarina: Sarcoptiformes). Paul C. Peterson, Warren T. Atyeo, and W. Wayne Moss. June, 1980. 142 pp.	15.00	16.50
22.	The Australian Crickets (Orthoptera: Gryllidae). Daniel Otte and R. D. Alexander. July, 1982. 477 pp.	45.00	47.50

SPECIAL PUBLICATIONS

		U. S Canada	Other
	Observations on the Genus Unio by Isaac Lea. Vol. II, republished in 1938. 24 plates. Unbound. 152 pp.	75.00	75.00
3.	Gabb's California Cretaceus and Tertiary Lamellibranchs. Ralph B. Stewart. 1930. 314 pp.	15.00	17.00
4.	New names introduced by H. A. Pilsbry in the Mollusca and Crustacea. William J. Clench and Ruth D. Turner. 1962. 218 pp.	10.00	12.00
5.	Guide to the manuscript collections in the Academy of Natural Sciences of Philadelphia. Venia T. and Maurice E. Phillips. 1963. 553 pp.	15.00	17.00
6.	Annotated bibliography of Quaternary shorelines (1945-1964). Horace G. Richards and Rhodes W. Fairbridge. 1965. 280 pp.	11.00	13.00
7.	Guide to the microfilm publication of the minutes and correspondence of the Academy of Natural Sciences. Venia T. and Maurice E. Phillips. 1967. 92 pp.	7.50	8.50
8.	Catalogue of Invertebrate fossil types at the Academy of Natural Sciences of Philadelphia. Horace G. Richards. 1968. 222 pp.	13.00	14.50
10.	Annotated Bibliography of Quaternary Shorelines (Supplement 1965-1969). Horace G. Richards and others. 1970. 240 pp. PAPERBACK	14.00	15.50
	CLOTH	17.00	18.50
11.	Annotated Bibliography of Quaternary Shorelines (Second Supplement 1970-1973). Horace G. Richards and others. 1974. 214 pp. PAPERBACK	21.00	23.00
	CLOTH	24.00	26.00
12.	Changing Scenes in Natural Sciences, 1776-1976. A Symposium to Commemorate the Bicentennial of the United States, sponsored by the Academy of Natural Sciences of Philadelphia. 1977. 362 pp.	27.00	29.00
13.	Zoogeography in the Caribbean. Frank B. Gill (ed.). 1978. 128 pp.	7.00	8.00
14.	Catalog of type specimens in the Ichthyological collection of the Academy of Natural Sciences of Philadelphia. Eugenia B. Böhlke. 1984. 246 pp.	15.00	17.00
15.	Morphometrics in Evolutionary Biology: The Geometry of Size and Shape change with examples from Fishes. F. L. Bookstein, B. Chernoff, R. L. Elder, J. M. Humphries. G. R. Smith, and R. E. Strauss. 1985. 277 pp. PAPERBACK	15.00	16.00
	CLOTH	23.00	24.00

1.48-1.64

ISBN 978-1-4379-5538-5

9 781437 955385